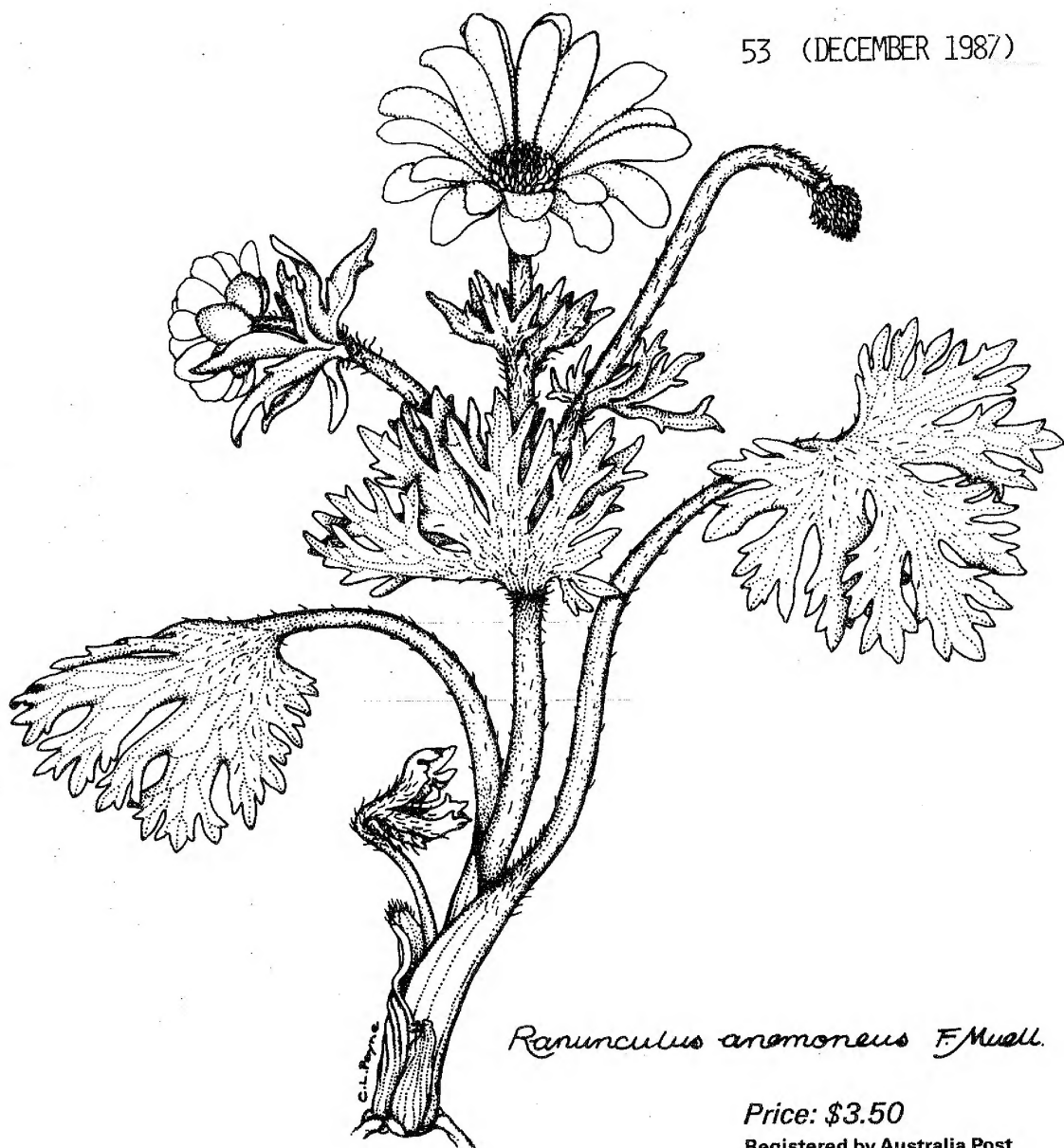




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IN DEFENCE OF MELALEUCA DIOSMATIFOLIA

L. Pedley

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The defence of Melaleuca erubescens (Wilson 1987) raises issues important enough to be considered further by professional botanists. Like the compiler of Index Kewensis I shall continue to use the name Melaleuca diosmatifolia because I do not believe there is an orthographic error to be corrected. Plainly M. diosmatifolia is not a homonym of M. diosmifolia and no amount of jesuitry will make it one.

I suspect that most practising taxonomists, Dr Wilson and myself included, would fit Ben Jonson's description of Shakespeare, 'thou hadst small Latin, and less Greek'. Consequently botanists tend to accept widely used plant-names without investigating their etymology too closely. Such a course is a proper one, since the chief aim of the International Code of Botanical Nomenclature is the provision of a stable method of naming taxonomic groups, avoiding and rejecting names which may cause error or ambiguity, or throw science into confusion. One of the principles of the Code is that scientific names of taxonomic groups are to be treated as Latin regardless of their derivation. Nowhere in the Code is it prescribed that a name should mean anything. In fact the name of a genus may be composed in an absolutely arbitrary way. Many names do not have a Latin form (for example, Acacia catechu, Melaleuca cajuputi and Ptilotus marduguru), some are almost meaningless (for example, Bossiaea bossiaeioides and Lycopersicon lycopersicum), and some are meaningless except to the cognoscenti (for example, Acmena resa and Syzygium wesa). After considering these points, I maintain that the epithet diosmatifolia is and should continue to be considered Latin, and that the name Melaleuca diosmatifolia cannot be changed to make it a homonym of M. diosmifolia.

Baron Dumont de Courset has been dead some 160 years so we cannot know what he intended. Since he had an interest in cultivated plants it might be reasonable to assume that he was aware of Andrew's earlier name, M. diosmaefolia. It is listed in the second edition of Hortus Kewensis. Not wanting to repeat the name exactly he treated diosma as analogous to the Greek derma and stoma and coined a Latin word diosmatus, -a, -um.

Neither can we know what the other dead authors, invoked by Wilson, recognised but did not 'explicitly spell out'. Cheel actually cited as a synonym of M. erubescens Otto, 'M. diosmifolia Dum. Cours. in DC'. He seems not to have seen the original description nor to have been aware of the original spelling M. diosmatifolia. Bentham also fell back on de Candolle. After his brief description of M. ericifolia var. erubescens he wrote 'M. diosmifolia, Dum. Cours. according to DC. l.c.,'. Seemingly, however, both de Candolle and Otto would have agreed with the argument advanced by Wilson. De Candolle put the name M. diosmifolia Dum. Cours. in synonymy of M. erubescens. I have not seen the protologue of M. erubescens but accept the statement of Byrnes (1986:266) that Otto also treated Dumont de Courset's name as a synonym. Whether he gave it in its 'corrected' form I do not know. It is also possible that de Candolle had not seen the protologue of M. diosmatifolia either, and merely followed Otto.

Orthographic errors come in various shades. The change of Wahlenbergia limnophylax to W. limenophylax is acceptable to most. The change was made by the author himself shortly after the original publication and his explanation is plausible (Lothian 1947). The rather arbitrary change of Eucalyptus nubilis to E. nubila (Johnson 1962) has passed with scarcely a comment though I am surprised that, in a genus where hybrids abound, nubilis ('marriageable') should be considered an 'inapplicable' epithet. Cassini's change, without explanation, of his generic name Brachyscome to Brachycome nine years after its publication has also been widely accepted though the original form was used by Eichler (1965). Bentham's change of Acacia omalophylla to A. homalophylla has also been accepted by some despite the advice of Stearn (1973:263) concerning the spiritus asper. Stearn could not be said to have little Latin and less Greek. On the other hand some names appear eminently correctable, but remain unaltered. Gnaphalium pensylvanicum is acceptable though the state of Pennsylvania and William Penn both have -nn-. Pandanus stradbrokeensis has not been 'corrected' though Stradbroke Island and Lord Stradbroke both have only gone -o-.

I have no idea how many names might be considered to be in need of correction. None of them is worth detailed analysis and discussion. A simple solution is available. Botanists should accept the original spelling of the name. The only exception would be the change of connecting vowels ae to i, and o to i and the reverse. Rare cases of having to decide on alternative spellings in protologues are usually easily settled, as was done by 't Mannetje (1977) for Stylosanthes guianensis. If original spellings were adopted, professional and amateur botanists would seldom be in doubt about the spelling of a name and time would not be wasted in sterile debate - such as this one.

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BLUE DEVIL - ERYNGIUM OVINUM A. CUNN. REINSTATED

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I have previously indicated that the Australian native plant, commonly known as Blue Devil, is different from the Chilean plant, Eryngium rostratum Cav. and that it should be referred to E. ovinum A. Cunn. (Michael, 1981). Candolle (1830) described the two species separately but he had not seen specimens of E. ovinum. Benthams (1866) included E. ovinum as a synonym of E. rostratum but did not clearly state that he had seen Chilean specimens. Wolff (1913) appears to have followed Benthams treatment, his description of E. rostratum being based entirely on Australian specimens, the Chilean material at his disposal being inadequate. Reiche (1902) described E. rostratum as very variable and referred to its occurrence in Oceania which I take to include the Australian region, the only part of Oceania mentioned in the distribution given by Wolff.

Authors of Australian floras have also followed Benthams treatment. In the latest edition of Flora of South Australia (Jessop and Toelken, 1986) there is, however, a note that it is unlikely that our plants and the synonyms (including E. ovinum) are conspecific with the South American E. rostratum sensu stricto. Auld and Medd (1987) have taken up the name E. ovinum and Kloot (1984), in a list of species, disjunct between southern Australia and other mediterranean or temperate regions, indicated that E. rostratum had been used in error for the endemic E. ovatum (sic).

After a close examination of the description and plate of E. rostratum in Cavanilles (1801), Chilean specimens held in F, GH and US, including part of the type collection (F), the type of E. ovinum (K) and much Australian material, I consider that, despite their variability, the Australian and Chilean plants are each worthy of distinct specific status.

The spreading inflorescence of E. rostratum is yellowish-white, with the largest (primary) heads up to 2.5cm long (excluding bracteoles) on peduncles up to 5cm long. None of the specimens I have examined show the sky-blue involucre bracts mentioned by Reiche (1902).

The inflorescence of E. ovinum is suffused with metallic blue and the primary heads are rarely as long as 1.5cm on peduncles no more than 2.5cm long.

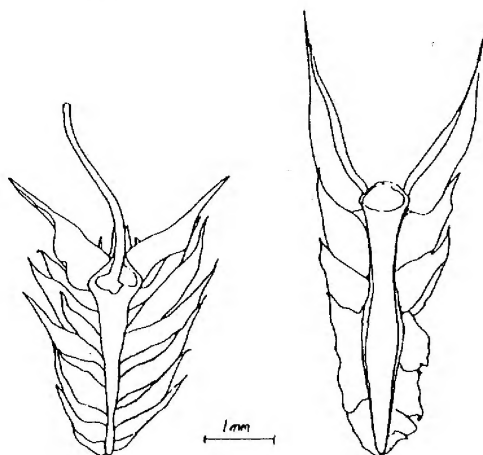
In both species the fruits are covered in membranous, vesicular scales. At maturity the fruits split into two mericarps with calyx segments attached. In flat facial view the mericarps show short, broad upturned scales in E. rostratum and long, narrow upturned scales in E. ovinum (See Figure).

The lowermost radical leaves are sharply serrate becoming lacinate towards the apex in E. rostratum (Cavanilles, 1801) while they are pinnatifid with long, linear, narrowly acuminate lobes in E. ovinum (Burbidge and Gray, 1970 as E. rostratum).

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Mericarps of *Eryngium* spp. kindly drawn by G.K. McDonald. Left: *E. ovinum* - from specimen collected by Michael, Rhyanna, near Goulburn, N.S.W. Feb. 1984 (CANB). Right: *E. rostratum* - from specimen collected by Claude-Joseph 3964, Curepto, Chile. Jan. 1926 (US 1283694).

ORBEA HAW. OR STAPELIA L. (ASCLEPIADACEAE): A CHOICE OF GENERIC NAME FOR THE NATURALISED CARRION FLOWER

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Species of the tribe Stapelieae (Asclepiadaceae) are exclusively stem succulents, and occur from southern Africa, through east Africa into the Arabian Peninsula, Mediterranean basin and the Indian subcontinent with one species in Burma (White & Sloane, 1937). Taxa of the tribe are popular in cultivation among succulent plant hobbyists in Australia. One species, *Stapelia variegata* L., has been listed as naturalised in the Australian flora (Hudson, 1985; Pearce, 1986; Stanley & Ross, 1986).

It is now generally recognised that the groupings of species into genera, as listed by White & Sloane (1937), were unnatural, being biased towards gross coronal morphology, and ignoring useful character combinations of vegetative morphology and the form of the pollinaria. A rearrangement of generic groupings was initiated by Leach (1975, 1978) and has resulted in some 7 new genera being described (Leach, 1978; Gilbert, 1980; Bruyns, 1981; Lavranos & Bleck, 1985; Plowes, 1986) with the revival of 5 generic names (Leach, 1978, 1980, 1982; Gilbert & Raynal, 1980; Bruyns, 1983) not recognised in White & Sloane (1937). Many of these genera are somewhat narrowly circumscribed (many with 1-3 species) and Walker (1982) has protested the splitting, suggesting instead a single genus Stapelia to cover the entire tribe.

Both Leach (1983) and Bruyns (1984) have defended their concepts and, as noted by Leach (1983), genera such as Stapelia L. sensu stricta (Leach, 1985) and Huernia R.Br., containing 43 and 50 plus species respectively, are hardly small. Whether or not all of the small genera will be accepted in the long term remains to be seen. However, Orbea is well defined with respect to Stapelia sensu stricta and the two genera may be distinguished as follows:

1. Stems & follicles glabrous, leaves absent, corolla with annulus
----- Orbea
- 1: Stems & follicles pubescent, leaves present, corolla without annulus
----- Stapelia.

It is recommended that the name Orbea variegata (L.) Haw. be adopted for the material naturalised in Australia. A full synonymy may be found in Leach (1978).

Orbea variegata (L.) Haw., Syn. Succ. Pl. 40 (1812).

Stapelia variegata L., Sp. Pl. 1: 217 (1753).

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EPIZOOTIC BLINDNESS IN GOATS FOLLOWING CONSUMPTION OF *STYPANDRA GLAUCA*:
A COMMENT AND A REQUEST.

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A paper on epizootic blindness in goats by
R. Whittington, J.E. Searson, S. Whittaker and J.R. Glastonbury
(NSW Department of Agriculture, Regional Veterinary Laboratory,
Wagga Wagga, NSW 2650) is reproduced below.

"Twenty seven goats out of a mob of several hundred became permanently blind after heavily browsing *Stypandra glauca* ("nodding blue lily"). Other animals were temporarily depressed and reluctant to move around. Blindness resulted from entrapment of the optic nerve within the optic canal during a phase of severe oedema of white matter throughout the central nervous system. Histologically the retrobulbar optic nerve was oedematous, the intracanalicular optic nerve was fibrosed and the optic nerve/tract further "downstream" was characterised by astrogliosis and Wallerian degeneration. Retinal photoreceptor degeneration was evident ophthalmoscopically by multifocal pigmentary abnormalities and histologically by loss of photoreceptors with hyperplasia of retinal epithelium.

S. glauca has not been associated with toxicity in livestock before; however, *S. imbricata*, which grows only in Western Australia, causes an identical syndrome.

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Main, D.C. Slatter, D.D., Huxtable, C.R., Constable, I.C. and Darling, P.R. (1981). Aust. vet. J. 57:132."

Reproduced from the Aust. Soc. Vet. Pathol. Annual Conference Proceedings BS.1:1987.

Another report of the same case in no. 15 of the Newsletter of the Australian Society for Veterinary Pathology (Jan. 1987) stated that 420 Angora wethers of mixed age were involved and 50% were affected in some way.

The above interesting items were brought to my attention as a result of my treatment of Stypandra in Flora of Australia 45, published last May. When preparing that account, I was not convinced (on the specimens available to me) that the Western Australian plants, then called S. imbricata R.Br or S. grandiflora Lindley, were specifically distinct from the eastern ones of S. glauca R.Br. despite their disjunct distributions. Hence, with a certain amount of apprehension, I lumped them all under the latter name, something that had been done by several botanists over the years including Mueller and Maiden, but not those in Western Australia at that time.

Despite their similar morphology, I had the feeling that the Western Australian plants, which are known as Blind grass, might prove to be specifically distinct from the eastern ones because they are proven toxic to livestock whereas those in the east were not considered toxic. There also appeared to be chromosomal difference between the two groups. The findings of Whittington et al. that eastern and western plants can cause an identical syndrome removes one of those distinctions and suggests these plants represent only forms of the one species. More work, therefore, needs to be undertaken to assess the chromosome complements of further Western Australian and Eastern Australian plants to see if a distinction based on chromosome numbers truly exist.

I would be interested to undertake further counts. Anyone caring to send me material for cytological study should fix young flower buds in 3:1 absolute ethanol/glacial acetic acid for 12-24 hours then store them in 70% ethanol. Material can then be sent to me drained of liquid and sealed in a plastic sleeve or envelope to my address above. Any material would be gratefully received.

NEW RECORDS IN THE NATURALISED FLORA OF SOUTH AUSTRALIA

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Abstract

Five naturalised species previously unrecorded for South Australia - Calepina irregularis, Anthyllis barba-jovis, Tragopogon hybridus, Iris xiphium and Agropogon littoralis - are briefly described. Extensions of the known range or status of 18 other alien species are cited.

INTRODUCTION

The Agriculture Department, through its Animal and Plant Control Branch, provides a plant identification service which was developed to its present throughput of approximately 1000 specimens per year chiefly by Mr C.R. Alcock. Dealing directly with landholders, agronomists and the authorised officers of Animal and Plant Control Boards, this service receives many specimens of naturalised plants representing species unrecorded in the literature and previously unpublished range extensions.

The following records are supplementary to the Flora of South Australia, 4th edn (1986). In describing the status of alien species the terminology of Kloot (1987) is followed. 'Naturalised' is a general term for alien plants growing spontaneously. An 'adventive' plant is one persisting without human help at one or a few locations, generally for less than 25 years and reproducing sparingly; when it has become widespread over a large part of the State or locally abundant in one or more regions and reproduces freely it is said to be 'established'.

ADA is an informal abbreviation for the Agriculture Department herbarium.

AIZOACEAE

* - Galenia pubescens (Ecklon & Zeyher) Druce var. pubescens; Jessop, Fl. S. Aust. 1:195 (1986).

Additional records from Mt Gambier and Pinnaroo extend the range of this species to the SE and MU regions respectively. Both are small populations which are likely to have originated from seed carried on vehicles or livestock, and G. pubescens may be regarded as still adventive in these regions although established elsewhere in the State.

Specimens examined: Pinnaroo showgrounds, 16.x.1986, A.R. Edwards s.n. (ADA 8944); Mt Gambier, adjoining saleyards, 6.v.1987, A. Kurray s.n. (ADA 9418).

PAPAVERACEAE

* - Argemone subfusiformis Ownbey subsp. subfusiformis; Toelken, Fl. S. Aust. 1:364 (1986).

This species now occurs locally in the SE region at Mt Gambier and in pastures near Millicent; its establishment in this region appears inevitable from its distribution in South Australia (Toelken, loc. cit.) and Victoria (Willis, 1972).

Specimens examined: Hundred of Mayurra, Section 84, 14.i.1987, D. Guerin s.n. (ADA 9178); Mt Gambier, 18.viii.1986, D.E. Moss s.n. (AD).

HYPECOACEAE

* - Hypocoum pendulum L; Toelken, Fl. S. Aust. 1:373 (1986).

More established in this State than was suggested by Jessop (1977) and Toelken, (loc. cit.), having been collected in the NL region (Appila) and at three locations in the YP region; at Minlacowie it was abundant through a 20 ha barley crop.

Specimens examined: Hundred of Moorowie, 16.x.1986, R.A. Bishop s.n. (ADA 8941); Hundred of Minlacowie, Section 238, 24.viii.1982, D.J. Cooper s.n. (ADA 5229); Hundred of Tickera, Section 125, 24.ix.1966, B. Copley 660 (AD 96701052); Hundred of Tickera, 15.x.1966, B. Copley, 772

(AD 96703013); Appila, 5.ix.1983, A.V. Wurst s.n. (AD 98512029).

CRUCIFERAE Tribe BRASSICEAE

* - Calepina irregularis (Asso.) Thell. in Schinz & Keller, Fl. Schweiz. edn 2, 1:218 (1905); Myagrum irregulare Asso. Syn. Stirp. Arag. 82 (1779).

Annual to 80 cm high, glabrous. Stems ascending or decumbent, branched from the base, ribbed. Basal leaves shortly petiolate, obovate to oblanceolate, lyrate-pinnatifid to sinuate. Cauline leaves sessile, elliptic to lanceolate, entire or shallowly dentate, 1-4 cm long, 2-12 mm wide, amplexicaul with acute patent auricles. Racemes erect, to 30 cm long; pedicels arcuate, to 5 mm long. Sepals ovate, spreading, c.1.5 mm long. Petals white, the inner pair 2.5-3 mm long, the outer pair shorter. Silicula ovoid with a short conical beak, 2.5-3.5 mm long, reticulate-rugose, 1-seeded, indehiscent, brown. Seed c.1.5 mm diam., smooth.

Native to Europe (Ball, 1964) and previously unrecorded in Australia. One large population is known in pastures at Yorketown, YP region, where it has spread rapidly in the 8 years since it was first observed. Flowering occurs from early September to mid October.

Calepina superficially resembles certain Euclidieae such as Neslia with indehiscent few-seeded siliculae. However, the fruit of this genus is comparable to a segmented siliqua (as in Raphanus and Rapistrum) reduced to a single fertile segment with a sterile beak.

Specimens examined: Hundred of Melville, Sections 91/92, 26.xi.1985, T. Voigt s.n. (ADA 8367); Hundred of Melville, Sections 91/92, 16.x.1986, R.A. Bishop s.n. (ADA 9409; AD; MEL).

CRUCIFERAE Tribe EUCLIDIEAE

* - Euclidium syriacum (L.) R.Br.; Hewson, Fl. S. Aust. 1:393 (1986). This species is a weed problem in pastures on at least one property at Yorketown, having persisted at this locality for at least 24 years despite attempts to control it and is manifestly more established than suggested by Hewson (loc. cit.).

Specimens examined: Yorketown, 10.ix.1986, R.A. Bishop s.n. (AD 98638272); Yorketown, 1963, n.coll. (AD 96344120).

* - Myagrum perfoliatum L.; Hewson, Fl. S. Aust. 1:408 (1986). The range of this established alien now includes the SE region, where it was accidentally introduced with seed from Yorke Peninsula. Specimen examined: Hundred of Lochaber, 1.xii.1986, E.S. Hogg s.n. (ADA 9080)

RESEDACEAE

* - Reseda odorata L.; Pearce, Fl. S. Aust. 1:417 (1986). Recently recorded from the NL region where it was abundant in a vineyard.

Specimen examined: Clare, 4.v.1987, T. Yeatman s.n. (ADA 9412).

LEGUMINOSAE Subfamily PAPILIONOIDEAE Tribe LOTEAE

- * - Anthyllis barba-jovis L., Sp. Pl. 720 (1753).

Shrub to 1 m high. Stems terete, sericeous, developing scaly light-brown bark. Leaves alternate, shortly petiolate with dilated bases, imparipinnate with 11-19 narrow-elliptic to narrow-obovate leaflets, sericeous and green above, densely silver-sericeous below; stipules minute, caducous. Inflorescence terminal, pedunculate, capitate, subtended by short trifoliate bracts, 10-25 flowered. Calyx 4-6 mm long with narrow-triangular teeth shorter than the narrow-campanulate tube, whitish-sericeous. Corolla light-yellow; standard obovate, 7-10 mm long, exceeding the other petals. Stamens monadelphous. Pod 1-seeded, indehiscent, included by the persistent calyx.

Native to the Mediterranean region (Cullen, 1968) and formerly grown as an ornamental; now adventive in the EP and SL regions of S. Aust. Flowering occurs in September to October.

Specimens examined: Port Lincoln airport, 7.ix.1986, P. Sheridan s.n. (AD 98625094); Port Lincoln airport, 19.ix.1986, P. Sheridan s.n. (ADA 8891; AD; MEL); Largs North, coastal dunes, 2.x.1967, T. Smith 528 (AD 96929033).

OXALIDACEAE

- * - Oxalis compressa L.f.; Jaspars, Fl. S. Aust. 2:709 (1986).

Now recorded from the NL region where it was abundant in a wheat crop; had been growing at the locality for at least 50 years.

Specimen examined: Wirrabara, 6.vii.1987, P. Smith s.n. (ADA 9469).

EUPHORBIACEAE

- * - Eremocarpus setigerus (Hook.) Benth.; Weber, Fl. S. Aust. 2:744 (1986).

This species should be regarded as established in South Australia as in addition to the localities cited by Weber (loc. cit.) it is widespread in the NL region where it is commonly called Fish weed or Drought weed.

Specimens examined: Bowmans, 10.ii.1981, R. Britton s.n. (ADA 4990); Hundred of Balaklava, Section 73, 18.ii.1987, G.W. Roberts 08 (ADA 9263; AD).

Agriculture Department files record other collections of this summer-growing annual in 1962 (9 km SE of Bowmans), 1963 (Balaklava), 1964 (Bowmans; Balaklava showground), 1972 (Balaklava), 1978 (Port Wakefield) and 1986 (Snowtown); voucher specimens for these records are lacking.

- * - Euphorbia falcata L.; Weber, Fl. S. Aust. 2:750 (1986).

This species has recently been collected from the YP region where it occurred with E. helioscopia in pasture and cereal crops.

Specimen examined: Hundred of Para Wurlie, Section 254, 14.i.1987, D. Cooper s.n. (ADA 9173).

THYMELAEACEAE

- * - Thymelaea passerina (L.) Coss. & Germ.; Threlfall, Fl. S. Aust. 2:865 (1986).

Thymelaea passerina is now present in the MU region, where it was recorded as a serious weed over 15 ha of a cereal crop in 1986.

Specimen examined: Hundred of McPherson, Section 30, 16.xii.1986, J.C.W. Jolly s.n. (ADA 9136).

Agriculture Department files also record two occurrences on arable land in the YP region, at Price in 1964 and Dowlingville in 1969; voucher specimens are lacking.

UMBELLIFERAE

- * - Conium maculatum L.; Eichler, Fl. S. Aust. 2:987 (1986).

Now locally naturalised in the EA region over 400 ha of a creek floodout; may be expected to be confined to similar moist habitats within this generally arid region.

Specimen examined: Manunda Station, 15.xii.1986, M. Michelmore, 108 (Herb. M. Michelmore).

SOLANACEAE

- * - Physalis viscosa L.; Symon, Fl. S. Aust. 3:1252 (1986).

Recently recorded in the NL region on a former garden site.

Specimen examined: Hundred of Kapunda, Section 1404, 12.v.1987, R.W. Webb 30 (ADA 9422).

SCROPHULARIACEAE

- * - Misopates orontium (L.) Raf.; Barker, Fl. S. Aust. 3:1300 (1986).

Now established and widely distributed in S. Aust. in crops, pasture and home gardens, with recent records from the FR, EP and SE regions.

Specimens examined: Hundred of Booleroo, Section 51, 10.vi.1987, D. Cousins s.n. (ADA 9447; AD); Cleve, Hundred of Mann, Section 94, 9.vi.1987, I. Honan s.n. (AD); Kingston, 12.ii.1987, L.R. Smith 61 (ADA 9254).

COMPOSITAE Tribe HELIANTHEAE

- * - Bidens pilosa L.; Cooke, Fl. S. Aust. 3:1434 (1986).

This species is adventive at several localities in the Riverland, MU region. These populations are small, on irrigation blocks, and in each case regarded by the landholders as a weed new to their area; they may be due to repeated introductions from New South Wales where the species is widespread.

Specimens examined: Waikerie, 1.iv.1987, C.J. Hamdorf 45 (AD); Fenwick Road, Berri, iv.1987, H. Patterson s.n. (ADA 9427).

Agriculture Department files also record collections determined by C.R. Alcock, in 1983 (Renmark), 1984 (Morgan) and 1985 (Waikerie); voucher specimens are absent.

COMPOSITAE Tribe SENECEIONEAE

- * - Senecio pterophorus DC; Lawrence & Belcher, Fl. S. Aust. 3:1597 (1986).

In addition to the distribution listed by Lawrence & Belcher (loc. cit.), S. pterophorus is still present in the KI region, as evidenced by recent collections. It had become established on Kangaroo Island by 1963 (O'Neil, 1962) but was almost eradicated by an active campaign during the following decade (Alcock, pers. comm.).

Specimens examined: near Kingscote, 23.xii.1986, D. Heaney s.n. (ADA 9125); Kangaroo Island, 21.i.1987, D. Heaney s.n. (ADA 9211).

COMPOSITAE Tribe CICHORIEAE

- * - Cichorium intybus L.; Cooke, Fl. S. Aust. 4:1640 (1986).

This established species also occurs in the EP region where it is occasional on roadsides.

Specimens examined: Hundred of Caralue, Section 24, 9.i.1987, R.J. Carter PL-226 (ADA 9167); road near Whyalla, 1.x.1984, I. Honan s.n. (ADA 7659).

- * - Tragopogon hybridus L., Sp. Pl. 789 (1753).

Annual to 70 cm high, glabrous, slightly glaucous. Stem erect, few-branched near the base, finely striate, green. Basal leaves few, linear, soon withering. Cauline leaves linear to narrow-lanceolate, subamplexicaul, acute, to 20 cm long. Peduncles to 10 cm long, erect, naked, inflated below the capitulum. Involucral bracts 8. Ligules oblong, shorter than the involucre, lilac-pink. Outer achenes somewhat curved, fusiform, 3.5-5 cm long; pappus of 5 unequal scabrid awns 0.7-2 cm long. Inner achenes straight, fusiform, c.2.5 cm long; pappus of plumose bristles c.2 cm long.

Distinguishable from the widespread biennial T. porrifolius by the pappus of the outer achenes. Native to southern Europe (Richardson, 1976) and previously unrecorded in Australia. A small population was found in pasture at Salter Springs, NL region, but the history of its introduction is unknown. The species may occur elsewhere in the State undetected due to confusion with T. porrifolius.

Specimens examined: Salter Springs, 6.i.1987, J. Hannay 1-87 (AD).

LILIACEAE

- * - Nothoscordum gracile (Aiton) W.T. Stearn
N. inodorum auct. non (Aiton) Nicholson; Jessop, Fl. S. Aust. 4:1764 (1986).

Established in the MU region as a weed of gardens and urban waste ground, extending the range cited by Jessop (loc. cit.).

Specimens examined: Hundred of Bookpurnong, Section 99, 12.xi.1984, J.D. Garvie 5 (ADA 7700); Loxton Public Library, 7.v.1987, J.D. Garvie 76 (ADA 9420); Lameroo, 27.ix.1983, J.W. Price s.n. (ADA 6862); Borrika, 15.vii.1985, G.J. Stasinowsky s.n. (ADA 8123); Loxton drainage reserve, ix.1983, S.G. Wheaton s.n. (ADA 6926).

IRIDACEAE

- * - Iris xiphium L., Sp. Pl. 40 (1753).

Evergreen perennial to 70 cm high with bulb; rhizome absent. Basal leaves linear, 20-60 cm long, 2-5 mm wide, glaucous; cauline leaves shorter and wider. Stem erect, unbranched. Cymes reduced to 1 or 2 flowers. Spathe bracts herbaceous, lanceolate. Flowers long-pedicellate, brown-purple, scentless. Perianth tube 1-3 mm long; outer lobes spathulate, 5-6 cm long, glabrous with a straining patent claw and a shorter decurved suborbicular lamina with an orange blotch; inner lobes oblanceolate, erect, 5-6 cm long. Style branches oblong, c.4 cm long, with acute crests. Capsule clavate, beakless. Seeds angular, yellow-brown.

Native to south-western Europe (Webb & Chater, 1980); introduced to Australia as a garden ornamental, and recently collected as an adventive on a roadside at one locality in the NL region.

Specimens examined: Barossa, 1985, n. coll. (AD).

GRAMINEAE Tribe TRITICEAE

- * - Elymus elongatus (Host.) Runem.; Jessop, Fl. S. Aust. 4:1882 (1986).

Introduced into South Australia for the stabilisation of eroding land and revegetation of salted areas. McPhie (1973) recommended the cv. Largo, seed of which had become available commercially following its successful use in Western Australia, N.S.W. and Victoria. E. elongatus is now adventive in this State, having been collected as small spontaneous populations on roadsides in the EP and SE regions in addition to the single locality, Keppoch, cited by Jessop (loc. cit.). Flowering occurs in December and January.

Specimens examined: Hundred of Campoona, Section 1, 28.i.1986, I. Honan s.n. (ADA 8568); Campoona, 15.i.1986, D. Lewis s.n. (ADA 8540); Hundred of Davenport, Section 1110 at Princes Highway, 16.i.1987, M. Michelmore 111 (ADA 9198; AD); Butcher's Drain outlet S of Kingston, 11.xii.1984, D. Morgan s.n. (AD 98592847).

GRAMINEAE Tribe AGROSTIDEAE

- * - Agropogon littoralis (Sm.) C.E. Hubbard, J. Ecol. 33:333 (1946); Polypogon littoralis Sm., Comp. Fl. Brit. edn 2, 13 (1816).

Perennial to 50 cm high with creeping rhizomes. Culms ascending, geniculate, simple or few-branched near the base, smooth, glabrous. Leaves glabrous, somewhat glaucous; sheaths loose; ligules 3-6 mm long, membranous, obtuse; blades linear, acute, flat, 2-8 mm wide. Panicle erect, 3-16 cm long, dense, with short whorled branches; branches and rhachis scabridulous. Spikelets 2-3 mm long, laterally compressed, 1-flowered. Glumes equal, narrow-elliptic, 1-nerved, scabrous, persistent, acute or produced into a straight capillary awn to 1.5 mm long. Lemma elliptic, erose-truncate, 1-2 mm long, membranous, glabrous, 5-nerved, with a subterminal capillary awn to 2.5 mm long. Palea elliptic, shorter than lemma. Anthers 3, c.1 mm long.

An intergeneric hybrid between Agrostis stolonifera L. and Polypogon monspeliensis (L.) Desf., this grass is male-sterile with abortive pollen (Hubbard, 1968). Native to saline habitats in southern and western Europe (Tutin, 1980); also recorded from Victoria, where

occasional around Melbourne (Willis, 1962). Now locally established at Port MacDonnell in South Australia, where it is common over pastures (formerly sown to Lolium and Trifolium) which have become salted due to seawater moving inland via drains. Flowering is recorded in February and March.

Specimens examined: Port MacDonnell, 13.iii.1987, A.E. Hincks 115 (ADA 9310; AD).

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ABLO REPORT

JOTTINGS FROM THE ABLO'S QUILL

Before I left Australia in August I think I succumbed to pressure from the Editor and promised that I would send news items or any other matters that might be of interest to members of the Society for the Newsletter. It seemed a good idea at the time! As it turns out it has been a fairly eventful period since I began here at Kew as the Australian Botanical Liaison Officer.

One Friday night in late September a minor disaster of the type any herbarium curator has nightmares about, took place here in Kew. A 1 1/2" water pipe burst early on a Saturday morning in the basement of one of the wings of the herbarium (Wing C). By the time it was found there was c. 40 cm of water on the floor, ironically being contained in the

wing by the barrier to keep the River Thames out! So the bottom row of boxes on the shelving was rather damp to say the least. Also, some boxes which were only in that basement temporarily, were stacked on top of each other and as the lower ones soaked up the water they collapsed and the higher ones fell into the pond. The Keeper, Mr Gren Lucas, managed to locate about 20 staff members who worked all day Saturday to remove as much of the soaked material as possible from the wing. The rest of us of course were slightly surprised when we arrived Monday morning. That week was spent attempting to dry out most of the soaked specimens, matching labels which had soaked off and trying to put material back into the correct order. Fortunately a lot of labels had actually stuck to the underside of the sheet above, and so not a great many were totally lost, although many det. slips did go down the drain.

Most of the specimens held in the basement at Kew is "overflow" material from the main collections, but there was nearly 100 boxes of specimens, primarily Snowdon's Sorghum collections, stacked there as an interim measure. In the end, of the 20,000 affected specimens only 13 have been lost altogether; a total of 367 boxes were ruined. Many specimens have had to be remounted and it will be weeks or months before the herbarium completely catches up, but the total loss is much lower than one would expect having seen the soggy, dripping specimens with loose labels. Of course, the affected specimens cannot be used for some work, such as pollen studies, but from all other respects they are intact. The activity and cooperation of all the staff here in the herbarium during the drying and cleaning up phase after the flood was refreshing and pleasing to be a part of.

Construction work is presently progressing (very noisily) in the central quadrangle of the herbarium where another basement is being installed. In fact, the burst pipe causing the flood was a new connection made late Friday afternoon by contract workers associated with the construction work. This new basement is to house c. one million specimens. The flood has of course stimulated many discussions about the use of basements in herbaria in general and specifically the question of what material will be placed in Kew's new basement area.

From all accounts the rather wild storm, or hurricane as some call it, which hit the south of England on the night of 15th October, was well reported in the Australian press. It was a very depressing sight the next morning to see the number of trees that had been destroyed. Especially as the 18" thick walls of the old church in which we live had given us a rather protected view of the storm - we didn't even close all the windows and a visitor staying with us slept through the whole thing - and we certainly weren't expecting anything like the devastation around us or to find the neighbour's fence wrapped around our front door. In the area near us (south-west of London) a large number of old oaks, beeches and walnuts were blown over and most of the roads and railway systems blocked for at least 24 hours. In fact it took several days before the few chain saws available had been used to clear all the roads. Our area was not as bad as some. We didn't even have a power cut - other places were out for a week or more. The electricity people said that it was because of the huge distances involved and the remoteness. Some of the worst affected villages were 'up to several miles' from the main grid!

The comments I have received from Australians about the damage at Kew implies that the media might have played things up a little - who would have ever imagined such a thing. Certainly the loss in Kew Gardens

themselves was great and is estimated to be about 10% of the trees (i.e. about 1000). Approximately 400-500 of those were actually blown over in the storm with the rest being split or so badly damaged that they have to be felled anyway. The major part of the gardens is still closed off as there is a great deal of clearing up still to be done, so I haven't been into much of them since the storm. The damage from the storm was much greater further south of London and so the number of trees lost at Wakehurst Place, the satellite 200 ha Botanic Gardens in Sussex, was far higher than here at Kew. It is estimated that between 50% and 60% of the trees there have been lost. The amazing and sobering thing is that hundreds of years of growth were terminated and destroyed in two or three hours. Apparently 2 million trees were destroyed in about 4 hours in the County of Kent, and the latest figures for the south-east of England is 15 million.

The major loss is of trees of historical significance, rather than of scientifically valuable species now considered to be rare or threatened either in the wild or in cultivation. For instance, the largest Himalayan Holly (Ilex diphyrena) in the country was lost from Wakehurst Place. While this species is relatively rare in cultivation it is, happily not so in the wild. Fortunately, there don't appear to be great losses of rare species, although the specimens of Malus trilobata, now a rare apple in the wild, were destroyed.

Closer to the herbarium here at Kew I'm afraid the large Zelkova carpinifolia (Caucasian elm) which sheltered the front of the building was one of the casualties. Remarkably it fell right alongside the herbarium and caused no damage to any structures. Those of you who have visited the herbarium will remember this magnificent old tree, planted in 1760 or 1761, and believed to be the oldest tree lost in the storm. It was right outside my window and I had already become quite attached to it, as I'm sure the past few ABLO's who sat in this same bay did. I certainly preferred the leaves rustling on the window to the better lighting conditions we now have. Fortunately there are some other Zelkovas of the same vintage still standing in the gardens.

Well, the storm certainly caused terrible devastation, but what is happening in its aftermath? Of course replacement of many of the trees, in areas like Kew Gardens and Wakehurst Place and in the countryside in general, requires careful thought and planning. For the past 15 years Kew has had a policy of obtaining and collecting propagation material (particularly seed) of many of the older trees in the Gardens from wild populations all over the world. Thus, some replacement plants will be available from Kew's own nursery and the propagation team have also been busy vegetatively propagating from many of the trees lost or damaged as a result of the storm.

These natural disasters usually have some positive spinoffs and opportunities have not been lost in converting the damage to some advantage through a number of scientific projects already in progress. For instance, workers are looking into root micro-organisms and root development in relation to tree diseases, biochemists from the Jodrell Laboratory are investigating the potential of certain compounds for pest control, others are interested in the growth rings not only for the normal seasonal variation but also to determine if there are any differences or correlations in growth from the north and south aspects of the tree, and of course timber samples are being collected.

Another legacy of the storm is the large amount of timber lying around the countryside. Six weeks after the storm much of it still lies

on the ground where it fell. Kew should stand to make some financial gain from the trees lost in the Gardens, some of it being of the rarer expensive sought-after furniture woods. Now that the Gardens are run as a trust such avenues of revenue collection are significant. Apparently there are to be timber auctions for the larger pieces of timber and craftsmen are to have access to the smaller specimens.

So, even though there has been an enormous loss at Kew the storm has (obviously) really only speeded up the natural attrition rate. My own feelings have changed from amazing depression and disbelief to a more optimistic view derived from these constantly changing plants on which we work. Kew Gardens has set up a Hurricane Fund to which you can contribute by writing to the Director, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB.

On October 14 I visited the Liverpool Museum for the official opening of a special exhibition associated with the Australian Bicentennial. The exhibition, Australia 1788 - A Mine of Botanical Novelty, was opened by the Australian High Commissioner, His Excellency, The Right Honourable Douglas McClelland. A viewing of the exhibition itself was followed by a rather good spread for lunch with Australian wines and pavlova for dessert! A separate report on the Liverpool Museum exhibition appears elsewhere in this Newsletter.

My own work is progressing fairly well. Some of the Kew staff seem to find it rather amusing that an Australian botanist is going to do field work in the U.K. I have arranged to spend some time in the field next spring and summer with Mr Peter Sell from Cambridge to help me sort out some of the problem Spergularia species. Peter is an expert on the British flora and the opportunity is too good to miss. A number of spergularias have been introduced into Australia from Britain and Europe and it is important to understand the species here before we can be anywhere near certain of the relationships of the taxa in Australia.

Judy West
Australian Botanical
Liaison Officer

AUSTRALIA 1788 - A MINE OF BOTANICAL NOVELTY

"Upon the whole New Holland, though in every respect the most barren country I have seen, is not so bad that between the productions of sea and land a company of people who should have the misfortune of being shipwrecked upon it might support themselves, even by the resources we have seen."

Sir Joseph Banks' general opinion after travelling along
2000 miles of coastline of eastern Australia.

The special exhibition at the Liverpool Museum, 'Australia 1788 - A mine of botanical novelty', highlights the contrast of the difficulties of the first few years of settlement in this 'inhospitable land' New Holland with the wealth of information on the aborigines, plants and animals which returned to Britain during the following decades.

The exhibition is linked to the Australian Bicentenary celebrations and aims to show what the pioneer colonists discovered when they arrived in Australia, as well as their impressions and reactions to their new environment. It also clearly illustrates the interest of the early colonists in the strange and fascinating flora of their new land and the impact of the early explorations and discoveries back in Britain. The Museum has taken the opportunity to use its wealth of scientifically important plant specimens (among other material), formerly in the herbarium of the Liverpool Botanic Gardens (see Austral. Syst. Bot. Soc. Newsletter 36: 1-3 (1983)) to "reflect on our historical, cultural and family links with Australia".

The use of the settlers' own words, extensive photographs and many natural history specimens gives the exhibition a lively and realistic flavour. The whole display is of a very good quality and provides a broad spectrum to cater for viewers with varied interests. As an Australian botanist and latter part of the exhibition concerning the 'Back to Britain' phase of the early explorations was the most interesting. This section shows the enthusiasm of British naturalists for animal and plant collections from this new continent. In a country where there was an unprecedented interest in natural history this material became prominent not only for scientific investigation, but also for its weird curiosities.

The Museum is to be congratulated on the excellent standard of the exhibition. In particular, The Keeper of Botany, Dr John Edmondson and Dr Angus Gunn, also of the Botany Department, should feel proud of the product of their many hours of careful research. Their enthusiasm for the subject is reflected in the style and manner in which the exhibition is presented.

'Australia 1788 - A mine of botanical novelty' will be on display at the Liverpool Museum until 24 April, 1988.

Judy West
Australian Botanical
Liaison Officer

BOOK REVIEWS

IDEAS AND ENDEAVOURS - THE NATURAL SCIENCES IN SOUTH AUSTRALIA

Edited by C.R. Twidale, M.J. Tyler and M. Davies,
Royal Society of South Australia, 277pp. 1986. \$28.00

The development of the natural sciences in South Australia occupies a very special place in discovery of many of the unique features of the Australian continent. While field scientists of the eastern side of the continent tended to investigate the higher rainfall areas of coast and tablelands, the South Australians had the arid and semi-arid lands on their doorstep and proceeded to explore and investigate. In later years they were involved in the scientific aspects of special problems like

those of the peculiar soils and of the trace element deficiency which stood in the way of agricultural and pastoral developments. We must be grateful to the Royal Society of South Australia, to the editors (Twidale, Tyler and Davies) and to the contributors for this useful and interesting account illustrated with many photographs and four coloured plates.

Much of the book is fascinating reading for it is inevitably about the people as well as science, field work under particularly difficult conditions and clashes of personality in both the amateur and professional scientists. The well-written introduction to the book encapsulates the interacting difficulties.

The different developments are described under nine chapters: Understanding Landscape (C.R. Twidale), Geology (D.W.P. Corbett, B.J. Cooper and P.M. Mooney), Soil Science (C.G. Stephens and K.H. Northcote), Agricultural Climatology (A. Marshall), Botany (E.L. Robertson), Plant Pathology (H.R. Wallace), Zoology (S.J. Edmonds), Medical Science (R.V. Southcott) and Anthropology (N.R. Tindale). The contributions are somewhat uneven in coverage for, as the introduction points out, some embrace the whole of the time period and even take account of the period of coastal exploration before settlement. The treatments accorded earlier and later work also differ. There remains so much of interest and value that these unevennesses are not too important. For serious and detailed further study, about 1200 references are given.

South Australia, in the nineteenth century and in the early years of this century, had a remarkably large share of Australians of distinction in science. Some are Howchin, Mawson and Madigan in geology, Prescott in soil science, Black, Osborn and Wood in botany, Johnston in zoology, Wood Jones in anatomy, zoology and anthropology, Brailsford Robertson and Marston in biochemistry and Cleland in everything, for he was pathologist, botanist, mycologist, anthropologist and conservationist.

One fascinating chapter is on the medical sciences: Southcott deals with the history, particularly clinical aspects, up to 1924. We are reminded of the difficulties of coping with diseases before our knowledge of bacteriology and of our understanding of hydatids, when Smith said in 1905 that "... this country rivals Iceland in its claim to be called the Land of Hydatids".

The roles of the various societies and institutions are dealt with in relation to the different subjects. The development (from 1921) of the Handbooks of the Flora and Fauna was unique to South Australia and provided a regular publishing outlet.

Botanists will be interested in much relating to plants in the different chapters but will be especially interested in that by Enid Robertson (no relation to this reviewer!). South Australia's large contribution to systematic botany in Australia is described. We are fortunate that J.M. Black, a migrant from Scotland in 1877, found botany his absorbing interest and, after a discouraging attempt to grow wheat in saltbush country, was able to devote his whole time to the flora, helped by money from his family. We should be grateful for the success of the Gilbert and Sullivan Operas for Black's sister, Helen, who had been secretary to D'Oyly Carte and later his wife, left a legacy to her brother which enabled him to continue his work on plants without financial worries.

The book contains much of interest and can be read with pleasure as well as being a reference for sundry important contributions to Australian science.

Rutherford Robertson

A key to the genera of New Zealand ferns and allied plants.

Brownsey, P.J. and Galloway, T.N.H. (illustration) 1987.

National Museum of New Zealand, Miscellaneous Series, Number 15. 31pp.
Wellington, New Zealand.

Publications such as this fill an important niche in botanical literature.

I am not a specialist taxonomist, let alone a pteridologist, but have on occasion taught students about ferns and their putative relatives. Brownsey and Galloway's book is excellent. It will make teaching elementary pteridophyte morphology and taxonomy very much easier.

The introduction makes it clear that the work is a guide, not another taxonomic treatment which requires linguistic skills beyond most people. Budding academic botanists and amateurs in both New Zealand and Australia will find the volume useful and readily understandable.

Galloway's excellent illustrations, with their accompanying legends, are just as important as Brownsey's text. Most students (and teachers!) find well-labelled illustrations more useful than descriptions. I would prefer to see the illustrations fully-labelled rather than having to refer to a series of legends for a description of the illustrations.

Brownsey's text has the major advantage of avoiding arcane pteridological terms as far as possible:- one of the great strengths of the volume as a teaching tool. As a result, the user need not cart a compound microscope and several dictionaries into the field in order to follow the keys to identify a specimen. A good hand lens and this volume alone will suffice.

I heartily recommend the volume to those who teach about, and to those who wish to become familiar with, New Zealand's rich fern flora without having to learn a whole new vocabulary in the process. It should also serve as a model for specialists in other plant groups who wish to make their work accessible to the greatest number of people. Taxonomists should remember that they are few and far between. Volumes such as this make a particular plant group understandable to 'laymen'. Such people, the 'non-taxonomists', make up about 100% of the population!

D.R. (Bob) Selkirk

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NOTICES

BOTANICAL HISTORY SYMPOSIUM

There are three Ansett airfares available at a reduced rate for anyone wishing to attend the Botanical History Symposium in May.

The price of the tickets will be slightly less than that for stand-by. Tickets should be Adelaide - Melbourne, Canberra - Melbourne, Sydney - Melbourne or Hobart - Melbourne return. If interested contact Phillip Short, National Herbarium of Victoria, Birdwood Ave., South Yarra, Vict. 3141. Telephone (03) 6509424.

P. Short.

A NEW HOME FOR HO

The long-awaited new building for the Tasmanian Herbarium is now a reality. During November the estimated 25 tonnes of collections, equipment and furniture were man - (and woman -) handled down several flights of steps (and very intermittently in the lift) from the old annexe on top of the Life Sciences building at the University of Tasmania into the purpose-built facility in the lawns below. The staff took up residence there at the beginning of December, and now face the task of finding where everything is in a welter of boxes and cartons of varying sizes, scattered through an unaccustomed large number of rooms.

The new building is single storied and set into a bank with lawns flowing over the roof and down both ends. Only the front facade, containing the offices and main work rooms is exposed. Floor area increases from 200m² to nearly 550m², with the major increase being in office space (6 instead of 2) and in collection storage area, where the number of compatus type units has increased from 11 to 29, with room for another 10 at a future date. The collections are housed in a vault (similar to those at AD), protected by an automatic Halon fire-extinguishing system.

We have taken the opportunity, while the collection was in disarray anyway, to make some re-arrangements. The Compositae, Gramineae, Cruciferae etc have all been changed to their respective "-aceae" terminations, resulting in re-arrangments within our alphabetical system. Similarly, changes like Acacia to Racosperma which also involved major relocations have also been incorporated.

The collections have been distributed throughout the new shelving and the process of splitting up overcrowded boxes, which was long overdue, has begun. We hope to have the collection back into an accessible state by the end of December, although it will be some months into 1988 before we will be back to anything like a normal routine. However, the threatened long disruption to the processing of loans etc now appears unlikely to be as severe as anticipated, and users can assume that normal services have been resumed.

The address (G.P.O. Box 252c, Hobart 7001) and telephone number ((002) 202635) of the herbarium will remain the same. For those wishing to physically locate us, the new building is still on the University campus, immediately above the intersection of Churchill Ave and College

Rd. Coming from the city, catch a Churchill Ave bus at Franklin Square and get off at stop 12A. Hours are officially 9 am to 5.20 pm, although there is usually someone in attendance from 8 am.

At the time of writing it was planned that the formal opening of the building would take place in early February 1988.

A.E. Orchard

FLORA MALESIANA - AN INTERNATIONAL SYMPOSIUM COMMEMORATING
Professor Dr. C.G.G.J. van Steenis.

From August 20 through 25, 1989, an international symposium will be organised by the Rijksherbarium in Leiden, The Netherlands, to report on progress in the Flora Malesiana project and to commemorate its founder, director, general editor and major contributor, Prof. Dr. C.G.G.J. van Steenis, who died in 1986.

The scientific program will focus on fundamental problems herbarium taxonomists and field botanists working on tropical floras are faced with in their day to day work. Special attention will be devoted to those diverse aspects which had Prof. Van Steenis's special interest: taxonomic delimitation, biogeography of Malesia, mountain floras, dispersal, nature conservation, and contributions from morphology, anatomy and phytochemistry to plant classification. Progress reports on individual Malesian plant families, some approached in a multidisciplinary manner will form an essential part of the program. Following the symposium a one-or-two-day Flora Malesianna workshop will be held at the Rijksherbarium for current and prospective contributors to the Flora.

All botanists with an interest in tropical floras are invited to attend. Those who wish to receive further information are kindly invited to write to me at Rijksherbarium, P.O. Box 9514, 2300 RA Leiden, The Netherlands.

P. Baas

THE REVISION OF FLORA EUROPAEA VOLUME 1

Flora Europaea, published in five volumes (1964-1980), is a synthetic catalogue, with keys and descriptions, of the vascular plants of Europe. Its publication has provided a relatively stable taxonomic and nomenclatural framework for the flora of the continent, and has stimulated much further research and publication. During the 23 years since the first volume was published, a high level of taxonomic activity in Europe has uncovered many species and subspecies new to science in Europe, new nomenclatural combinations, species new to the European flora that are already known elsewhere, and several recently naturalised adventive species. Taxonomy has flourished notably in floristically rich parts of southern Europe, and there has been a great increase in the available literature. A revision of Flora Europaea Volume 1 has thus

become necessary to incorporate new data and to update the original text, and to satisfy the continuing demand for a complete Flora of Europe.

The revision of Flora Europaea Volume 1 is being funded by a grant from the Flora Europaea Trust Fund of the Linnean Society of London. A Research Fellow (Dr J.R. Akeroyd) was appointed from 1 October 1983 at the Department of Botany, Reading University, under the Supervision of the Flora Europaea Editorial Committee.

The poster presents some statistics relating to the number of potential new entries (some 450) to the text of the revised volume, with examples of the sort of new information that is being accommodated. In practice, about one third of species and subspecies described new to science since 1964 have been treated in synonymy or as notes under other taxa. About 30 existing entries have been taken out on account of being erroneous or synonymous. Flora Europaea presents an overall, European view of species and attempts to resolve or reconcile opposing taxonomic opinion: its definition of species may be seen by some taxonomists to be too broad. There is also a considerable body of minor text changes required in the descriptions, chromosome numbers, ecological phrases and geographical data.

There will be an increase of some 10% in the text of Volume 1. The revision will be completed by the end of 1988, and the revised volume will be published by Cambridge University Press in 1990/91.

John Akeroyd

ASBS NEWSLETTER EDITOR

Helen Hewson wishes to resign as Newsletter Editor. Council is seeking a replacement. Please advise L.Haegi (Secretary) if you are interested.

L.Haegi

REQUESTS

WANTED: flowers, and both ripe and unripe fruits of Josephinia (Pedaliaceae) in order to complete a revision. The request comes from Dr H.E.K. Hartmann, Institut für Allgemeine Botanik und Botanischer Garten, Universität Hamburg, Ohnhorststrasse 18, D-2000 Hamburg 52, Federal Republic of Germany. Anyone able to supply or know where they can be obtained is asked to contact Dr Hartmann.

WANTED: Akaniaceae - flower buds, flowers, normal vegetative shoot tips in FAA and seeds. Needed for study of floral morphology and seed albumen by Dr Ursula Hofmann, Goettingen Institute, Systematisch - Geobotanisches Institut der Universität Goettingen, Untere Karspüle 2, D-3400 Goettingen, West Germany.

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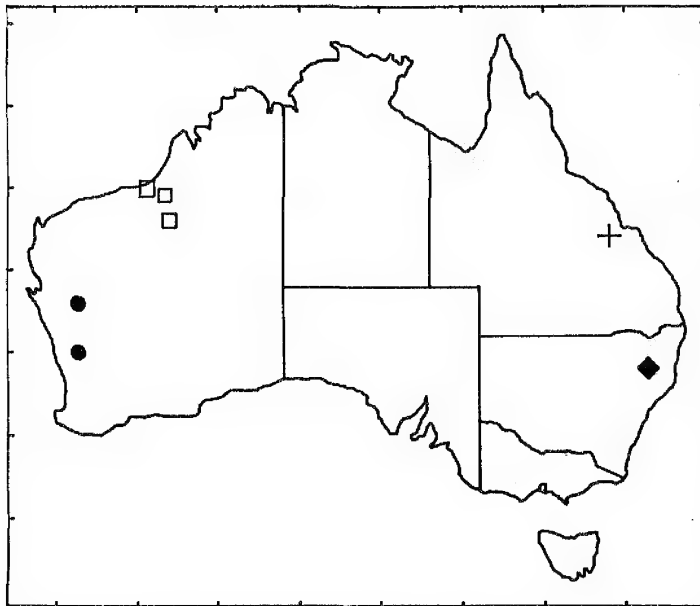
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THE CONCEPT OF THE GENUS

C. Jeffrey

Herbarium, Royal Botanic Gardens, Kew, UK.

The concept of the genus may be best approached by way of evolutionary epistemology, for the generic problem may be considered to be an epistemological rather than a biological one. Evolutionary epistemology is the comparative investigation of cognitive mechanisms and their phylogenetic development (Riedl, 1984). It interprets the a priori of the individual as the a posteriori of its evolutionary history. Evolution is a knowledge-gaining process which copies and modifies judgments on problems of structure and function within the particular selection-field of each species. The knowledge gained takes the form of genetic instructions - biological hypotheses and algorithms - selectively incorporated into the genome of the organism during its evolutionary history. In consequence, as Lorenz (1941, quoted in Riedl, 1984) stated, our forms of observation and categories, determined before any individual experience, are suitable for the external world for the very same reasons as those why the horse's roof, even before his birth, suits the soil of the steppe, the fins of the fish, even before it is hatched from the egg, suit the water.

One essential for a living organism is the ability to distinguish the like from the unlike - to separate the constant from the variable, to extract form from its manifestations, and to infer from one similarity to further ones. This unconsciously operating biological algorithm of comparison, by which the necessary decisions are taken in this respect, expresses itself in our ability to distinguish homology from analogy and thus to construct a system of classification based on the recognition of internally consistently-determined similarities.

It is remarkable that this algorithm, a functioning of those unconscious processing mechanisms which are the phylogenetic precursors of reason, should have operated so long and with such success without its mode of operation being understood. Its activities have produced what has been traditionally understood as the natural system, encompassing some 2 million species of living organisms and forming a factual basis for the very development of evolutionary theory. Not until the middle of the present century (Hennig, 1950) has a conscious methodology - cladistics - been developed to challenge, as yet imperfectly, the primacy of the pre-conscious intuitive method. Its development has followed a sterile period in which the very existence of any method was denied to intuitive systematics and attempts to relinquish the homology concept in comparison were made (Sokal & Sneath, 1963). It is amusing that the accusation of amethodology is now being repeated by the cladists!

The concept of the type, not as an archetype (nor in the nomenclatural sense), but as the totality of the characterizing or group-defining features of a taxon and their inter-relationships, both spatial and temporal, and its establishment for taxa of every rank from species up to kingdom, and the construction of the hierarchy of the taxonomic system itself, are other successes of the biological algorithm of comparison. The hierarchical nature of the system is a consequence of the fact that the order of the living is itself hierarchically structured (Riedl, 1978), and that selection has therefore endowed our unconsciously operating cognitive apparatus with the most adequate system for processing its patterns.

We can thus acknowledge the factual basis of the taxonomic system and its conformity to natural law, as has been demonstrated by Riedl (1978). Genera and higher taxa represent the correlated groups of features which have become fixed during evolutionary history, at first by burden and then through epigenetic interconnexions. There regularities - and the regularities of the genome that determine them - transcend the individuals that exhibit them and become ever more inclusive, basic and stable - and older - the higher the category of the taxon in the hierarchy. If constancy be taken as a criterion of reality, the genus has to be considered more real than the species, let alone the individual. Recognition of the genus, therefore, implies the recognition of the first level of unifying regularities above the species to which its status as a component of our environmental perceptions makes it advantageous for us to assign a distinct, individually-designative name. Two sets of variables are thus involved in the recognition of the genus - the extent of the unifying regularities, and the relative advantages to our dealing with the world of applying a generic name, employed in the designation of individuals (as opposed to a serial, subsectional, sectional, subgeneric or subtribal name, not so employed) to a given manifestation of such regularities. The solution lies in the maximalization of the utility, i.e., the information-content, of the classification. In the case of certain east African members of the tribe Senecioneae of the Compositae, for example, the information-content and thus the ability of extrapolation (or predictivity) are both enhanced by the recognition as distinct genera of Crassocephalu^m, Emilia, Solanecio, Kleinia and Gynura as compared with the inclusion of them all in a broadly-circumscribed Senecio, or, on the other hand, the division of, say, Crassocephalum, into 2 or more distinct genera. The former course would obscure the organization of similarities within the total similarity-field, the latter would artificially disrupt a component sub-field. In the case of Emilia, the adoption of two subgenera has provided the most practically useful treatment.

In view of its origin in the pre-conscious, as discussed above, it is no surprise that the generic concept is as old as the development of spoken language, and no doubt evolved into the realm of conscious reason along with that uniquely human characteristic (Bartlett, 1940). The grouping of distinguishable but similar kinds into genera facilitated the development in language of a flexible yet precise nomenclature for animals and plants. For most purposes of folk science, the undefined yet understood categories of genus and species sufficed, so that we find in common speech only these two are included in the plant nomenclature of most languages. Thus both the concepts and the binomial nomenclature that serves them have their roots in folk science. Their utility in facilitating ordering the living world into pragmatically useful concepts was thus carried over from the pre-conscious to the conscious. So useful has the generic concept since proved in classifying knowledge in different cultures of the world that its history parallels the history of the development of language and indeed of conscious thought itself. Our recognition of genera is a reflexion of the way in which our thought is adapted to the logical regularity of the world. It is no accident that the experiment undertaken by Anderson (1957) to test the taxonomic intuition of different taxonomists showed that they agreed in the concept of the genus (Uvularia) used in the experiment.

Implicit in the etymology of the word genus is its application to things akin by birth or origin, but so basic to human thought is the concept that not only has it been applied to classifications in other

sciences - e.g., mineralogy - in which there are no genetically-controlled genealogical relationships between the different observed kinds - or species, but has been adopted in logic to denote a class or kind of things which includes a number of subordinate kinds - again called species - sharing in certain common attributes. Conventionally, the idea the genus and species is considered to have entered biology by way of Aristotelian logic; evolutionary epistemology shows, that in fact the reverse is the case; it is a selectively-fixed component of our cognitive apparatus.

Why, then, do we have problems with the genus concept? One major contributory factor is historical. It is the fact that our scientific taxonomic system, which we apply to plants world-wide, is essentially a product of a local, European folk-taxonomy which has come to us by way of the Graeco-Roman cultural tradition and the historical and philosophical developments of 17th and 18th century Europe (Stafleu, 1969). This aspect has been treated in detail by Walters (1961) who points out for example, that 2/3rds of all the genera in the *Genera Plantarum* of Linnaeus are European. It is hardly surprising that this Eurocentric system proved inadequate to deal with the tremendous influx of new plants from outside Europe during the latter part of the 18th and especially the 19th centuries. One result of this inadequacy was the stretching of certain European - or at least north-temperate - centred genera into vast, unwieldy concepts far exceeding their original limits; in *Compositae*, *Vernonia*, *Eupatorium*, *Aster*, *Erigeron*, *Gnaphalium*, *Helichrysum*, *Matricaria*, *Chrysanthemum*, *Senecio* and *Centaurea* are well-known examples. Another result was the establishment, in an attempt to keep pace with the influx of material, of numerous small or monotypic genera based on some easily-observed morphological feature - in *Compositae* most often the pappus, examples of which in this family are abundant in the flora of Australia.

As Walters (1961) has shown, these processes together were responsible for the quasi-logarithmic hollow curve produced when the number of genera in a family with a particular number of species is plotted against the number of species in a genus. The largest genera, and the large number of monotypic genera, are both products of the taxonomy of the 19th century. Clayton's (1972) analysis shows the *Compositae* have been especially subject to recognition of small and monotypic genera. Both reflect the historical Eurocentric bias of systematics. Future progress will require consideration of genera on a world-wide basis. The large ones need to be examined to see what treatment - retention or some or other degree of splitting, will produce the most informative classification; the small ones require consideration in the context of their confamilials to ascertain whether or not generic types (or defining characters) need to be re-assessed so as, again, to produce a more informative classification. Given that plants carry information about the patterns in which the vegetable world is ordered, the task of systematics is to utilize that information in a way appropriate to the production of hypotheses of those patterns. Brooks (1981) demonstrated that the most satisfactory hypotheses will be maximally-informative, minimum-entropy classifications that reflect the causes of the ordering of the data into detectable patterns. If the cause has been evolutionary history, the classification will thus reflect it. Phylogeny then emerges, not as the basis of classification, but as an evolutionary inference from it. With this proviso, we can agree with Stevens (1985) that generic concepts which are such hypotheses of pattern will best serve the needs of biology, as they will best answer the questions biologists need to ask.

We are thus provided with a criterion for the delimitation of taxa, but not with one for the allocation of generic rank. The considerations of Estes & Tyrl (1982) may be helpful here. Other things being equal, taxa accorded generic rank should be comparatively easily recognizable, thus facilitating identification, and be utilitarian in their nomenclature, facilitating access to the information available for the included species by causing the least disruption of established nomenclature. Our generic concepts must be true to their historical and prehistorical origins. As Stevens points out, in systematics we do not deal in certainties or truths, but only in more-or-less well-supported ideas and hypotheses. By what methods can the congruence of our hypotheses with the patterns they reflect - and thus the information-content of our classifications - be most rapidly and cost-effectively maximized at generic level. I for one do not doubt that the biological algorithm of comparison, refined by 3.5×10^6 years of evolution and operating through our intuitive cognitive processes will retain, as in the past, its primacy in the practice of plant systematics.

One general problem, however, merits attention. If divergence events occur, as often in *Compositae*, by peripheral isolation, then one can postulate that a species which at time t_0 is defined by characters 1, 2, 3, 4 and 5 has by time t_1 evolved by peripheral isolation into, say 6 daughter species A-F of which A-E are defined respectively by characters 1', 2', 3', 4' and 5', and which by time t_2 have given rise to genera A-F. A classification at time t_2 of the taxa concerned expressed as a cladogram will then take the form of a poly-tomy in which genera A, B, C, D and E are characterised by synapomorphies 1', 2', 3', 4' and 5' respectively; the F-group, however, is characterised by no synapomorphies other than those characterizing the higher taxon (A-F) as a whole. It is an inevitable paraphyletic residuum.

I submit that this is a very general taxonomic problem and the realization of the objective existence of inevitably paraphyletic taxa might save a good deal of unprofitable searching for non-existent synapomorphies.

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Genera, what and why - some thoughts

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Much of the discussion over grouping and ranking criteria for genera ultimately depends on our attitude to the relationship between splits in lineages and what may be loosely called morphology - which includes here anatomy, development, phytochemistry, cytology, and the like. Organisms have a genealogy, but some think it cannot be detected using such morphological characters. If phylogeny is in practice detectable it seems to me that genera must be strictly monophyletic, including all and only the known descendents of a particular lineage. Monophyletic genera are needed in questions in comparative biology, and the various goals we often talk about for classifications in general - stability, predictivity, and the like - will almost incidentally also be best met if genera (and other higher taxa) are of this type. However, if phylogeny cannot be detected by such means, it becomes difficult to defend principles for recognizing genera.

My own attitude in this argument is that of an optimist - phylogeny is in practice detectable. However, we must not forget factors such as homoplasy, various methods of horizontal gene transfer, and the nature of plant development, which complicate discussion of the properties of phylogenetically-based genera. I do little more than mention some of these factors here; one in particular, cross-species gene transfer (Syvanen, 1984, 1985), may pose particular problems to the search for genealogy. In the rather minimally-documented discussion that follows - little I have to say has not been said before (see the papers in Bull. Torr. Bot. Club 67: 349-389. 1940; Chronica Botanica 14: 92-160. 1953; also, Clayton, 1983; Stevens 1985) - I shall discuss some attributes of phylogenetically-based genera. These include the relationship between such genera and information retrieval, predictivity, and stability. This last leads to a discussion about possible grouping criteria for genera. I shall then mention briefly aspects of the problem of genera if we are pessimistic as to the detection of phylogeny, and this in turn leads to the sketch of a possible linkage between our attitude to phylogeny detection, level of knowledge of characters, and theories of cognition. These last were barely mentioned at the meeting, although a comment rightly pointed out their possible relevance. This paper, then, has grown out of the one that I gave at Thredbo, and it has also benefited from airings since at New York and Harvard. I am extremely grateful to all involved in these discussions.

Before going further, it is clear that discussions about large genera might as well be about large phyla or large sections. Indeed, many of the arguments at the species level are the same. Genera do not have any particular status in our understanding of nature. Nevertheless, and partly

because of our propensity to reify things, we may be inclined to think that genera are more "real" than sections or tribes, for example. Also size per se has little to do with most of the discussion. I will return to these points. The size aspect of large genera is relevant if the resolution of a particular generic problem encountered in floristic work lies outside the area being treated; there will inevitably be tensions.

The optimist

As in any other science, if a systematist's work is to be utilisable by other biologists, classifications must be constructed in a way that does not run counter to theories we hold about the living world. Scientifically useful classifications will include groupings that show congruence, that is, isomorphism in pattern of relationship, with observations and theories in other disciplines. Congruence at all levels is our *raison d'être*.

Studies in comparative biology that involve any directional component of evolution, such as biogeography, much of ecology, and comparative development, will run into serious problems if we treat as monophyletic groups that are paraphyletic (some of the members of a lineage are excluded: Fig. 1A) or polyphyletic (descendants of independent lineages are placed in the one genus). There are of course other groupings of interest to us, for instance, functional groupings in general, including plant guilds and pollination types. At times these can be studied outside the context of a phylogeny, with which they are not congruent. Phylogenetic classifications cannot deal with all the "relationships" in which we may be interested simultaneously.

A knowledge of phylogeny is clearly needed to enable us to answer many biological questions, but does phylogenetic classification thereby become a desideratum? Some would say yes, and the discussion would end here. But let us consider phylogenetically-based genera in the context of the more traditional goals of classifications. These goals are not independent, since such desirable properties as efficient information retrieval and data summarisation are intimately connected with those of stability and predictivity. The first two deal with how we have handled the information we had available; the second two concern how new information relates to the old.

Information retrieval and data summarisation.

Information may be discussed in terms of characters; characters are the result of evolutionary change. There is much evidence that evolution can be considered, at a first approximation, as change with or without divergence of lineage; at least at the generic level. The algorithms used in phylogenetic analysis aim to minimize the overall amount of change when all the taxa and all the characters are considered together. That is, with characters like flowers red \rightarrow white, carpels 3 \rightarrow 4 \rightarrow 5, and phellogen superficial \rightarrow deep-seated, and these characters scored for 5 taxa, the algorithm will attempt to arrange the taxa so that the number of times flowers change from red \rightarrow white is minimized, at the same time producing a compromise (perhaps) because the aim is to do this with all the characters. Several changes may occur in one character if fewer changes are then needed for the others. This is basically parsimony, the relationship between data, algorithms for analysis, and results.

The result of the data analysis is a branching, tree-like diagram. Phylogenetic classifications are then based on these trees, and the information used in their production is effectively summarized in the most efficient way (given the constraints of the algorithm) so long as the taxa are monophyletic. Since monophyletic taxa are made up of the terminal taxa at the ends of all the bifurcations of a particular branch, the characters of that branch will make up the description of that monophyletic taxon. Unique derived characters will be mentioned only once (Farris, 1983, for references).

Classifications are effectively open-ended in this context. A non-unique character state will be unique at some higher level, at which time it will properly enter the description. Thus the character "superior ovary" should not be part of the description of the Clusiaceae, but only of that of a much higher level taxon. Reversals, parallelisms and the very nature of plant development do affect the issue here, as I shall mention shortly in the context of predictivity, but less than will be caused by wholesale adoption of paraphyletic groups. The current lengthy descriptions of genera are less efficient as summaries of variation than they might be. Paraphyletic taxa which have no unique features (but see below), will need extensive descriptions which effectively describe the absence of characters; they lack the unique features of the monophyletic groups removed from them. Making descriptions comparable then results in monophyletic taxa with equally lengthy descriptions. Also, generic descriptions often include variation characterising lower level taxa. This is akin to the covert recognition of paraphyletic groups - striking variation is discussed, but not recognized formally. Of course, such descriptions could be broken down into the characters of the genus and then an outline of the variation within the genus.

The problem is accentuated because we commonly use only three hierarchical levels - family, genus and species. The advantages of a hierarchical classification based on hierarchically arranged data come only when the two are congruent. If we try and combine information from different hierarchical levels, we will lose the advantages of this match.

Predictivity

In so far as a tree reflects phylogeny, it will also predict the distribution of other characters that reflect phylogeny. The issue of predictivity is complicated, however.

I shall use a modification of the diagram that gave rise to so much discussion at the meeting; others could be used and the arguments emended accordingly. Much change may have gone on in lineage A (Fig. 1: I will ignore what might constitute "much change"). Different arguments may then be made that genera A' and B' are more "predictive" than A and B.

1. Prediction of the distribution of undiscovered novel characters. A decision may be reached that more novel characters will be congruent with generic limits if A' and B' are recognized than if A and B are. Although no new characters may be congruent with B', characters at the basal node of that genus also occurring in A', several may be congruent with A'. A and B are both taxa with whose circumscription one would expect some new characters to be congruent, but perhaps not as many as if the paraphyletic/monophyletic genus pair is recognized.

2. The prediction of the distribution elsewhere of a character known only in one group. This will depend on the actual distribution of the character in that group, but if a character occurs in all members of the genus, there will be asymmetries in prediction. A character that is known only in B' should automatically occur in A' (barring reversals and the like), whereas characters only in A', A, or B may or may not occur in other genera. The reason for the more effective predictivity of genus B' is for the same reason that it was less effective in the first example! Prediction at higher hierarchical levels even in this case is most efficient in the context of hypothesised hierarchical relationships. Rather than searching in a paraphyletic genus C' for taxa with the properties desired, (Fig. 1A), one should look successively at members of genera C and D (Fig. 1B).

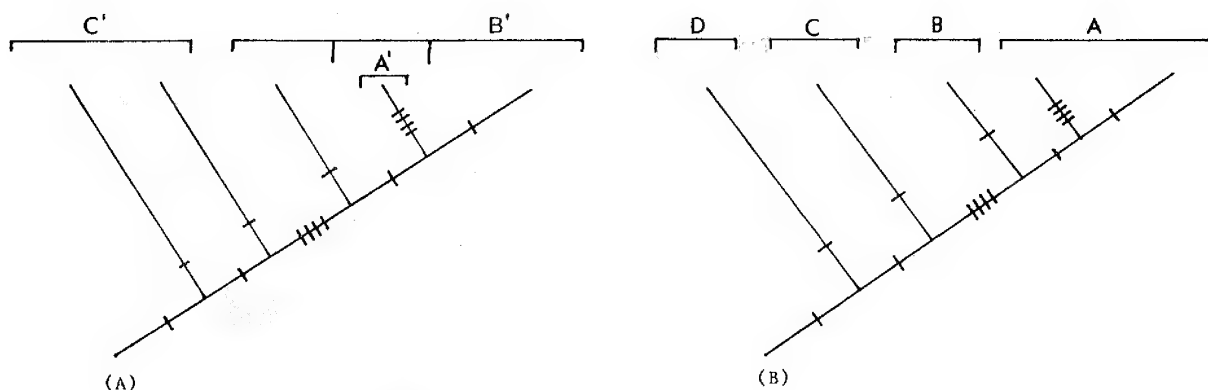


Figure 1

If parallelisms and reversals occur, the argument becomes more complex, but so long as phylogeny is detectable, the outline of the argument remains the same. In addition, the more that change in structure occurs by the switching of developmental pathways, rather than simple addition onto preexisting ones, the more may paraphyletic groups develop a measure of predictivity (sense 1). If character c, derived at the level of B', is replaced by c' at the level of A', then it could be argued that both A' and B' have unique characters. Also, if predictions are being made in the context of the search less for a particular character than the possession of features associated with that character, then the occurrence of such characters will reduce the predictivity (sense 2) of both monophyletic and paraphyletic groups.

3. Prediction of co-occurrence of characters in general. If we are predicting the co-occurrence of unique characters, the argument will be similar to case 1. If one simply wants genera that show maximum co-occurrence of any character, then this may depend on the size of the genus (see below) and its phenetic status.

We might also consider the distinction between phenetically and phyletically stated characters (I am grateful to Trevor Whiffen for an early morning discussion that clarified this for me). As an example of the former, consider prediction of the character "bird-pollinated flowers". It does not matter if the flower has 50 stamens or 1, a fused corolla or none, so a phylogenetically based classification in which such

distinctions do matter will indifferently predict (sense 2) this character. (It is unclear that a phenetically based system will necessarily be any better, unless based solely on this character.) However, even the character "bird-pollinated flowers" has phylogenetic overtones - only a subset of plants has flowers.

The important point of these apparently rather convoluted arguments is that what one may expect of predictivity changes with change in the relationship between taxonomy and phylogeny and also development and morphology, and what exactly is meant by "predictivity".

Stability

There has been much mention of the probable instability of phylogenetically based taxa. However, the stability of evolutionary classifications is bought at a price: although the groups recognized in them are uncertain as regards their phylogenetic status, predictivity, and information content, yet the methodology of character evaluation makes it hard to justify change in groupings.

As increasing details of phylogenetic relationships are discovered, it does not mean that nomenclatural changes will result. Providing that a genus remains monophyletic, this detail can be recognized at the infrageneric level, if so desired. Monophyly is a grouping criterion; it is largely silent about rank. Change in rank, or at least change in name, is necessitated only when there is a change in genealogical relationships such that it can be reasonably hypothesised that the current genus is paraphyletic or polyphyletic (this simply rephrases in a phylogenetic context a dictum of evolutionary systematics). Even then, appropriate adjustment of generic boundaries will minimize change in names (Bremer & Humphries, 1986).

We may wish our genera to be both monophyletic and "recognizable" - we make an appeal to perceptual salience and common sense - but one soon realizes that both are fluctuating quantities, with the former sometimes in short supply in plants and the latter in taxonomists! In any event, appeal to the senses for a ranking criterion can be made only so long as the requirement for monophyly remains paramount. However, because "evident" discontinuity in morphology or ecology can always be made to seem more important than any nomenclatural inconvenience, or vice versa, there seems to be no end to discussion as to whether two or more monophyletic sub-groups of a monophyletic genus are to be accorded generic status or not.

Note that smaller genera are not more "natural" than larger genera. If by "more natural" is meant "more things can be said about the group", small genera are more natural, but why not call pairs of species, genera, since more things can be said about these two species than can be said about all the members of a large genus? However, there is no particular reason why one can say more unique things about one hierarchical level than another - species, genus, or family - although parallelisms and reversals may cause a slight modification of this claim. All monophyletic taxa are equally natural in this sense.

Our short-term memory may indeed be most efficient when we try to memorize up to seven things (Miller, 1956), but that is hardly a reason for

recognizing small genera. Considering species as letters, we can memorize seven letters, words, or sentences almost equally well. Very large groups do seem unwieldy, however, and we may consider large size as grounds for dismembering taxa, and thus be prepared to admit smaller "evident differences" to enable us to carry out this butchery (a fairly common tendency in evolutionary systematics, too). It is almost as though each of us has a little equation in our heads as we consider generic rank - some product of the number of taxa in a group and the distinctness of that group has to be exceeded if it is to be called a genus. The trouble is, different taxonomists have different numbers in their heads.

The only ranking criteria that seem possible for higher taxa are based on age of the lineage or some aspect of similarity in the pattern of relationships shown by the taxa in different lineages, also probably ultimately based on age. It has recently been claimed that DNA hybridization in birds provides a way of determining both a genealogy and time elapsed since splits in lineages, a reclassification based on time has been suggested, and a claim made that the groups now recognized show broad congruence both with aspects of morphology and geography (Silbley & Alhquist, 1986). The prospect of an age criterion for determining rank perhaps appals, both because there would probably have to be different starting dates for different groups (or very widespread nomenclatural changes at higher levels) and also because there does not at this stage appear to be any broad congruence of patterns such as may occur in birds.

Even if we think our groups are unsuitable for phylogenetic analysis, there is still benefit in thinking phylogenetically. At the very least this should lead us to emphasize similarity, what holds things together, as much as or more than differences. Polyphyletic genera will be dismembered and monophyletic groups restored to the central core, important steps in understanding relationships. Emphasis on differences at the generic level leads to chipping away of groups from this central core, and will very often leave a paraphyletic residue. Many problems at the generic and family level have resulted from such a procedure. A monographic approach that emphasizes similarity may lead initially to the submerging of many names, since historically decisions as to generic discreteness have been based largely on gap size, and all too often made in floristic contexts.

The pessimist

Some may believe that only extensive application of techniques using restriction endonucleases, sequencing of DNA, and the like, will enable us to resolve phylogeny. Of course, this raises the interesting questions as to the nature of the relationship between evolution as splitting of lineages, and evolution as change of form. Why should there be these groups that are out there in nature?

The approach to the problem of generic rank and circumscription can still be in terms of hierarchical correlations and one can still end up with something very similar to phylogenetically-based classifications. This will be if there is a belief in some hierarchy of relationships out there, albeit not one generated by the splitting of lineages. If, however, one believes "real" relationships are like those between groups in some sort of multidimensional space, then there are going to be problems in constraining these relationships into the fewer dimensions of

the hierarchy. Discussion of things like predictivity will become even more difficult, because it will not be simple hierarchical predictivity that is at issue, but some sort of global and less well-defined predictivity. Genera can be based on level of linkage in a dendrogram, which would seem mechanical to some, or gap size, but gap size changes as new data are acquired.

Perhaps a way to justify genera in this situation is to appeal to how we use classifications. This is difficult, because one use can be played off against another and optimality for any particular purpose is unlikely, and any "general purpose" is inherently ambiguous. We might make an argument that because we do and have done things in a particular way, we should continue to do things in this way. In this case, there can also be little appeal made to the desirability of establishing a relationship between classification and causal science. It is also an unclear argument, because history suggests more variation in how we classify than is implied. But perhaps we classify in a particular way, because that is how we have been selected to think ("intuition" in another guise). Again, history negates the simple form of this argument, and, even looking at my own development, I cannot see that I intuitively recognize exclusively any particular kind of group.

Conclusion

Arguments about intuition or instinct immediately get us into deep and largely untrodden waters (cf. Saint Peter!) as to how exactly the mind functions, what are the constraints put on this functioning by evolution, can they be overcome, and the like. Answers are unlikely to be simple. Perhaps we can think in terms of particular ways of grouping organisms into genera developing from the interaction between the quantity and quality of the data at hand, how we are likely to treat differing kinds and amounts of data (whether or not we "instinctively" do this), how we want to analyze the data, and such mundane factors as to how tired or fresh we are. We know that the very act of perception is a complex operation in that what we see is guided to a certain extent by what we believe is there, and by the processing and compartmentalising of sense data before stimuli reach the brain. A sparsity of data may help lead to typological thought; large amounts of poor data may lead to a more phenetic approach, emphasizing quantity of difference over kinds; as the data improve an evolutionary and then phylogenetic approach become possible. Such a modest statement, which, however, has interesting implications, is broadly in line with recent work in categorization (e.g. Medin & Smith, 1984; M.J. Gordon, pers. comm.; see also Reznick & Kagan, 1983) and the historical development of systematics (Stevens, 1984).

Ultimately we cannot hope to produce very useful classifications at the generic or at any other level unless we can refine and extend our work at the very basic level

of collection of much more and better data. The more we can do this, the better our phylogenies will become, assuming they are detectable, with interaction between classifications and observations (as Colless, 1984, noted, this aspect of taxonomic thought has been somewhat under-emphasized of late). The result of the debate outlined above will in large part depend on the quality of our basic data.

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THE ROLE OF CLADISTICS IN GENERIC DELIMITATION

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INTRODUCTION

This paper is concerned with the question of whether the methodologies and principles involved in cladistics have any significant role to play in generic delimitation. Thus, cladistic theory and methodology are not the focus of this discussion, but rather I want to address whether the results of cladistics - i.e. hypotheses of phylogenetic pattern - are a useful or, as many would say, an essential component of historical analysis.

The literature reveals only a relatively small number of botanical cladistic papers which deal specifically with data sets investigating generic limits. Most of the studies appear to be within genera at the species rank, and some of course have been at the tribal and family level. I shall use a small number of published examples to assess the role cladistics might or might not play in determining generic limits.

The paucity of examples of cladistic studies at generic level is a reflection of the stage of cladistics that we have reached in botany - botanical cladistics is really still in its infancy. It is also very clear that there are difficulties in working at the generic level (compared with species) because of availability of data. To do a thorough analysis of several genera the worker must examine and sample every taxon within those genera, and in many cases this may involve several hundred species. This, of course, is not a function of cladistics alone; any analysis relies on complete data at the basic level of species. However, I do think it is partly responsible for the lack of already published cases of cladistic analyses at the generic level. The very nature of cladistics means the characters must be carefully interpreted and scored for every taxon. There are several cases in the literature in which character states have been wrongly assumed from already published morphological treatments of the groups, resulting in misinterpretations of homology. In other situations, in which genus, of 20-30 species, has been represented by a single species, has later been found to be variable for particular characters.

It is fairly difficult, if not impossible, to discuss the application of cladistic methodology specifically to generic delimitation. Thus, many of the comments made concerning cladistics I fully realise will be just as applicable at ranks other than genera and are not particularly peculiar to generic cladistics. This doesn't matter since the principles still apply.

PRINCIPLES OF CLADISTICS

If we look at the writings of cladists from Hennig to the present we can summarise the common theme into some basic principles of cladistics. Most will be well aware that the literature on the theory and method of cladistics is vast; my summary will be necessarily brief.

I think there are two main principles of cladistics: 1) taxa are united into natural groups on the basis of shared derived characters, or synapomorphies and 2) classifications must express these patterns of synapomorphy, i.e. only monophyletic groups should be recognised. Obviously the principle of monophyly is dependent on that of synapomorphy. The underlying assumptions in these 2 principles are generally acceptable to those using non-cladistic systematic methods. The recognition of monophyletic groups is central to systematics. The best way of inferring monophyly of a taxon is to show its components possess one or more shared derived character states or synapomorphies.

In addition to the two principles mentioned above the acceptance of strict parsimony is central to cladistics. The idea of parsimony is basic to all scientific reasoning, but it seems that cladists have been more concerned with the relationship between parsimony and systematics.

GENERAL ASPECTS OF CLADISTICS

Besides the basic features of cladistics (viz. synapomorphy, monophyly and parsimony) there are a number of general aspects, involving both advantages and disadvantages, which should be mentioned at this stage. Several will arise again in relation to discussion of the examples which follow.

Cladistics is a rigorous methodological discipline which makes one work within a rigid framework. It is a step-wise process allowing successive approximations and deductive reasoning. It allows one to evaluate alternative phylogenetic hypotheses in light of the knowledge of the taxa and characters concerned. Some cladists would say that the

greatest power of cladistic analysis is not that it is operational but that it provides us with a predictive hypothesis. The cladograms resulting from the analyses are working hypotheses which are falsifiable.

A cladistic analysis using the parsimony criterion usually results in several equally parsimonious cladograms. These must be treated as working hypotheses and evaluated in the light of the character state changes they specify. In choosing between alternative phylogenies one has to evaluate the various characters involved and favour those which you have interpreted with more confidence of those which have been studied in more depth. This amounts to a certain degree of a posteriori character weighting when choosing between alternative hypotheses.

Cladistics forces workers to observe and study characters and taxa in great detail, as many non-cladists have been doing in the past. This involves careful interpretation of homology and often reveals areas of discrepancy. In theory, as the information and knowledge of characters and polarities improves so the cladogram should be a better approximation of the evolutionary history of the group. New systematic data should also show the same phylogenetic patterns and nearly complete congruence with the cladogram.

In general the unevenness of a lot of data sets often restricts the generalisations that may be made from a proposed classification. In botany we are usually struggling with incomplete data sets particularly with respect to biological data, such as chromosome numbers or pollination or compatibility systems. Having produced a cladogram based on morphological data it is very easy in cladistics to superimpose another incomplete set of data onto the existing cladogram, whether this be done by + direct mapping of data sets or by a step-wise process such as functional outgroup analysis. This allows one to generate hypotheses of phylogeny with respect to particular characters, e.g. chemical constituents, and to predict unknown distributions of data.

Some workers maintain that the incorporation of information such as chemical, biochemical, molecular and cytological data is feasible and perhaps more appropriate in cladistics. We can often relate the constituents of one chemical class to each other in terms of their biosynthesis, i.e. sound hypotheses for biogenesis of natural products do exist. This means that it would be possible to determine plesiomorphic and apomorphic states of some of these products. Whether this is any better than any other data, such as morphological, is perhaps a matter for discussion.

Another aspect of cladistics is that a cladogram, even if not completely resolved, shows the relationships between the terminal taxa. This is an advantage over the many examples in the literature of non-cladistic classifications showing little relationship between groups.

Dealing with correlations of characters is a problem in cladistics, as in other forms of systematic methods, especially as an inherent part of cladistics is the assumption that characters evolve independently.

CLASSIFICATION

To place the discussion of the chosen examples clearly in context some general comments on classification are appropriate.

Systematists are concerned with two levels of grouping, i.e. the grouping of individuals into species and the grouping of these groups of individuals. Thus, there are only two categories, the species and the groups of species (Nelson and Platnick, 1981). Most would agree that the

species represent the units of evolution. So that, all higher ranking categories are just monophyletic groups of groups - it doesn't matter what we call them. An extension of this concept is that it is largely irrelevant to the cladist at what level the "groups of species" are recognised as long as they are natural (Funk, 1985). However, the quality of the group is important since the recognition of monophyletic or natural groups is the crux of cladistics.

EXAMPLES

In drawing on some specific examples from the literature I'm not going to discuss the methodologies of each analysis except to say that all used outgroup analysis to polarise characters, and the analyses were based on the parsimony criterion. I have selected particular points of interest from these studies as there is not time to discuss all aspects of the papers.

1. Carolin (1987) has recently completed a comprehensive study of generic limits in the Portulacaceae. There have been a number of revisions of individual genera in the family, but no critical review of generic limits over the whole group has been undertaken previously.

This Portulacaceae data set included 41 terminal taxa (25 presently recognised genera the larger genera were divided up into infra-generic groups to deal with the variability) and 40 characters. The preferred cladogram (Fig. 1) shows us that "some taxonomic adjustment is necessary". I have chosen only two examples to discuss, viz. Calandrinia and Anacampseros. The genus Calandrinia, comprising 11 terminal taxa, as it is presently circumscribed, is dispersed through several clades, and is therefore polyphyletic. Carolin suggested that Calandrinia s. l. be divided into five separate genera, all of which are strictly monophyletic.

If one follows Hennigian cladistic principles in that all sister taxa must be given equal rank, then recognition of CIST and AMAR as a genus means that it is illogical to maintain the genus *Silvaea* (SILV).

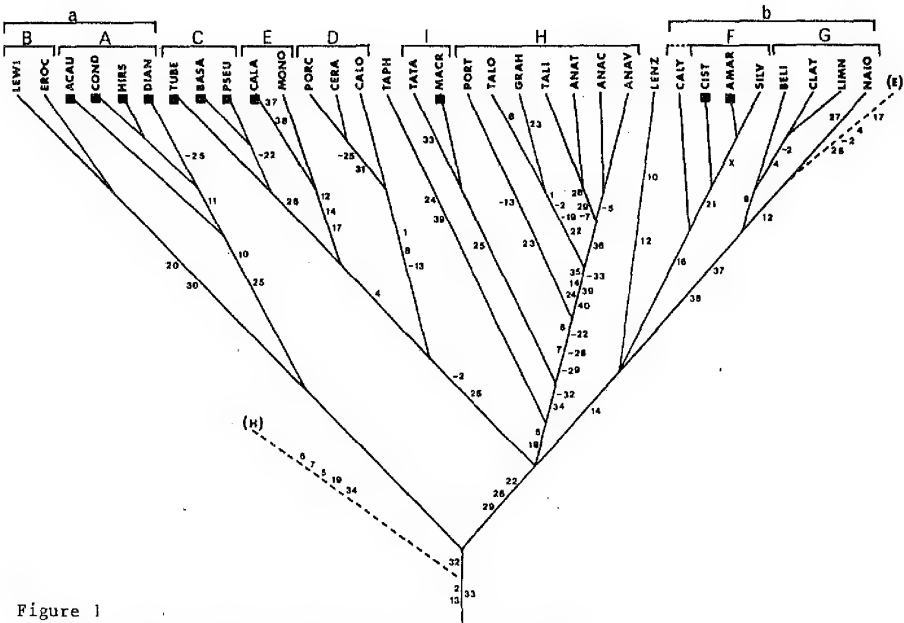


Figure 1

Cladogram of Portulacaceae from WAGNER algorithm. (See caption to Fig. 8). The alternative positions of clades E and H are indicated by the broken lines.

■ terminal taxa presently included in Calandrinia s.l.
Capital letters indicate consistent clades

Clade I which includes Calandrinia sect. Macrocarpae (MACR) and Talinum sect. Talinum (TATA) shows up some problems in Talinum. Talinum sect. Phemeranthus (TAPH) consistently failed to make a satisfactory clade with sect. Talinum. The investing aril of the former seems to be an important difference between the two sections, but the cladogram indicates that it is probably not strictly homologous with the investing "aril" (or unsclerotized testa) of the Grahamia group (char. 39).

The cladogram not only indicates that Talinaria (TALI), from southern U.S./Mexico, is very closely related to Anacampseros (there are no significant features separating these genera), but also that Anacampseros, included in the analysis as three sections more hoc insulso, itself is probably paraphyletic. Anacampseros sect. Tuberosae (ANAT) presently includes two species, one in Australia and another in Argentina. Although more detailed work on the seed structure and development is needed, Carolin suggested that it may be necessary to combine these two genera. The cladogram also suggests that it may be appropriate to combine the two African sections of the genus Anacampseros (ANAC & ANAV), and ANAT with Talinaria.

This analysis of the Portulacaceae illustrates the importance of cladistics in highlighting unnatural groups, polyphyletic and paraphyletic groups, and it also shows that cladograms can indicate possible errors of homology or interpretation of characters.

2. Funk's (1982) analysis of Montapoa (Compositae) provides us with an example in which the genus could possibly be divided into smaller units; but with a consequent loss of information. Within the cladogram for Montanoa (Funk, 1985, fig. 12) there are at least three clades, each defined by several synapomorphies, that could readily be defined as genera. However, grouping the species in this manner would leave large, non-monophyletic and undefinable groups. This treatment would result in the formation of two large paraphyletic groups, and consequently many nomenclatural changes. Also, it would suggest that the paraphyletic groups are evolutionary units, which is obviously not true.

3. Weston, Carolin & Armstrong (1984) performed a cladistic analysis of the two Rutaceae genera Boronia and Boronella, which form a monophyletic group within tribe Boronieae.

The resulting cladogram (Fig. 2), constructed using 32 morphological characters, showed Boronella (3 spp. from New Caledonia) together with one species of Boronia - B. koniambiensis (also from New Caledonia) to be a monophyletic group within Boronia. The remaining 92 spp. of Boronia, all of which are endemic to Australia, were grouped into three clades corresponding to sections within the genus. This hypothesis suggests that Boronia is paraphyletic.

In translating this cladogram into a classification the question of generic limits arises - do you recognise one genus or four? The authors, in their wisdom, made the decision to recognise Boronella (incl. B. koniambiensis) as a taxon within Boronia, rather than four separate groups.

With the existing cladogram, based on morphological characters, the authors were able to evaluate two previously proposed and differing hypotheses of cytoevolution in Boronia, by superimposing them onto the cladogram. Known chromosome numbers were plotted onto the cladogram, including the hypothesis that $x = 9$ is the base haploid number in Boronia. By this method it is feasible to examine the two cytoevolutionary hypotheses and decide which model provided the most parsimonious hypothesis of chromosome number evolution.

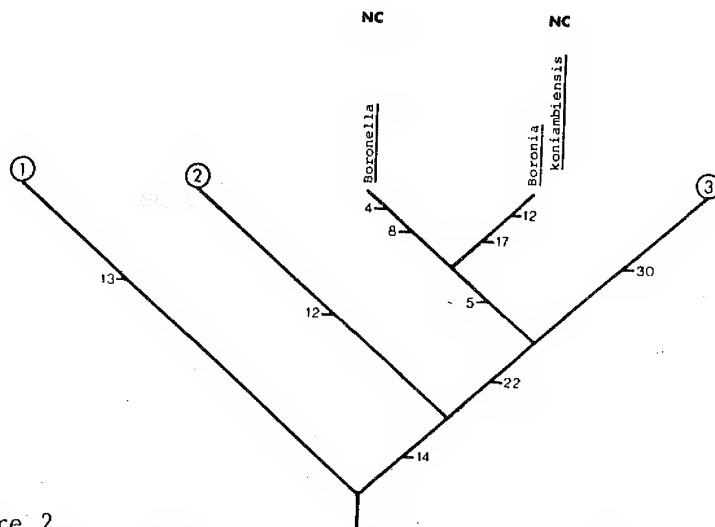


Figure 2

Cladogram showing main branches. (1) Section *Cyanothamnus* (sens. Wilson 1971); (2) section *Valvatae* (sens. Wilson 1971); (3) section *Boronia* s. lat. (incl. sections *Imbricatae*, *Boronia* and *Heterandrae* recognized by Wilson 1971). Single bars are synapomorphies of the characters as numbered in Tables 1 and 2. NC, New Caledonia.

4. The final example is that of a recently completed cladistic analysis of the three legume tribes, the Bossiaceae, Brongniartieae and Mirbelieae by Crisp & Weston (1987). The main aim of the analysis was to determine if the Bossiaceae, an endemic Australian group, is more closely related to the Brongniartieae, a tropical American group, or to the major Australian tribe, the Mirbelieae. While most of this project actually deals with the tribal level much of it is also relevant at the generic level. Crisp and Weston have studied the genera within the Mirbelieae and this has resulted in a number of them being redefined.

The Brongniartieae clade (Fig. 3) not only shows *Templetonia* to be polyphyletic, but also that most of the genus is more closely related to tropical American taxa (*Brongniartia* & *Harpalyce*) than to any other Australian genus. Crisp & Weston concluded that there is no good reason to separate the two major *Templetonia* species groups as separate genera, but that the status of *T. incana* and *T. biloba* is still uncertain (although it is clear that they can't be maintained in *Templetonia*).

The relationships within the tribe Mirbelieae are only partly resolved, and it is from this tribe that I have selected a further couple of examples. The genus *Pultenaea* with c. 160 spp. is shown here to be polyphyletic (Fig. 4). It is a very diverse genus and exhibits much homoplasy; even so the two larger groups of species share three synapomorphies, two of which are virtually unique stipule characters. Thus, retention of most of *Pultenaea* as a genus seems to be supported. None of the other smaller species groups separated from *Pultenaea* were reunited with the larger groups, and the authors suggested that probably all of them merit generic recognition.

Figure 5, with the details of one robust clade which occurred in all minimum-length cladograms for the Mirbelieae, indicates that *Oxylobium* is polyphyletic, even after the removal of a number of species, such as those placed in *Nemcia*. This is not an unexpected result since *Oxylobium* has historically been a dumping ground for species difficult to place elsewhere. It had been defined on plesiomorphies - high ovule number and absence of an aril. *Oxylobium* and *Gastrolobium* have been distinguished in the past on ovule number; Crisp and Weston have shown

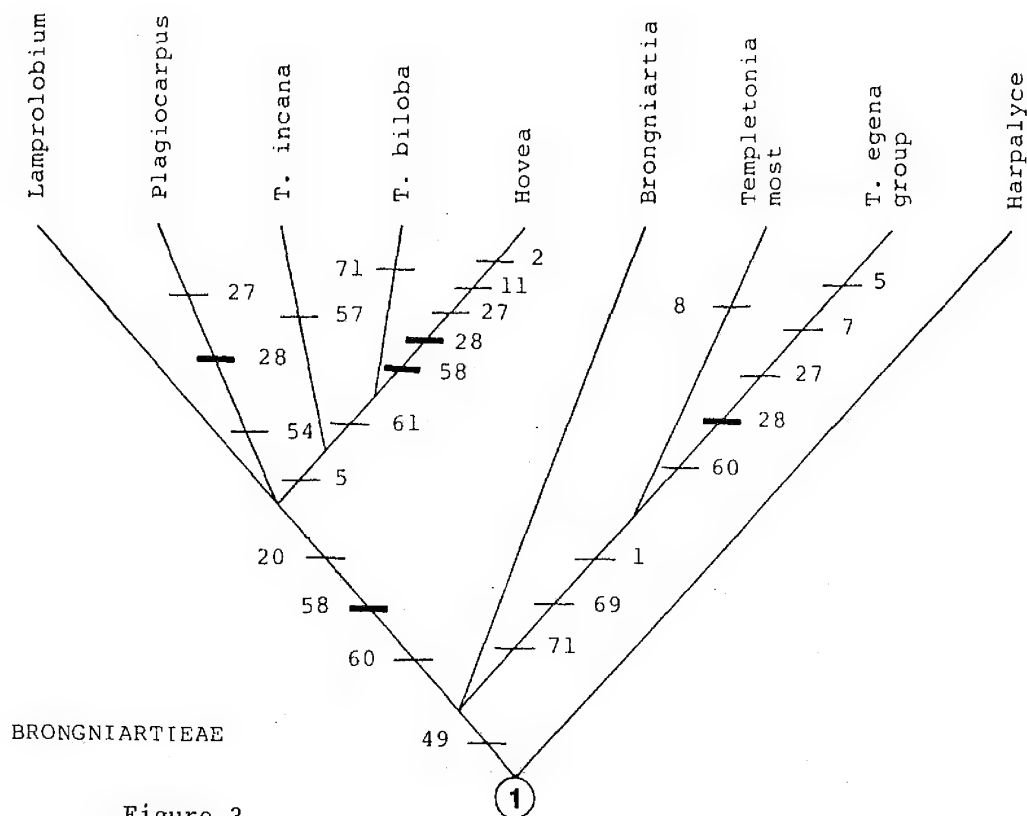


Figure 3

The preferred minimum-length cladogram of the Brongniartieae. For convenience of presentation, the cladogram is divided into several segments (Figs 10-14), which can be reconnected by matching the circled numbers and letters. The root of the tree is at the base of Figure 10a. Single step character-state changes are symbolised by bars, reversals by heavy bars, and multiple step changes by multiple bars. Full descriptions of the characters are in Table 3.

however that this character forms a continuum in these two groups (from 2-10) and is not a reliable character. The Gastrolobium - Oxylobium parviflorum group clade is formed on the basis of two synapomorphies, one of which is the presence of fluoro-acetate, which is unique in the papilionoids and which is considered to be highly significant. The authors united the O. parviflorum group with Gastrolobium.

The final part of the Mirbelieae cladogram mostly includes species of Mirbelia and Chorizema and indicates that these two genera are closely related. The circumscription of both genera remains a problem. The pectinate structure of this cladogram (Crisp & Weston, 1987, fig. 4) shows an example of "chaining", which is a problem in some cladistic analyses. In many cases this may tell you more about your characters and suggest that it may be appropriate to look more closely at some interpretations or homologies. They seem often to be associated with parallelisms or repeated reversals.

Because I have chosen selectively from this analysis it appears as though Crisp & Weston are proposing to carve up most of the Mirbelieae. However, of the 34 total number of genera, the cladistic analyses have shown that the majority of these genera (29) are monophyletic as previously defined. Not only have these analyses shown some genera to be unnatural, but they have also shown that a reassessment of characters can indicate the difference between grouping taxa on one or two obvious characters instead of on the basis of synapomorphies.

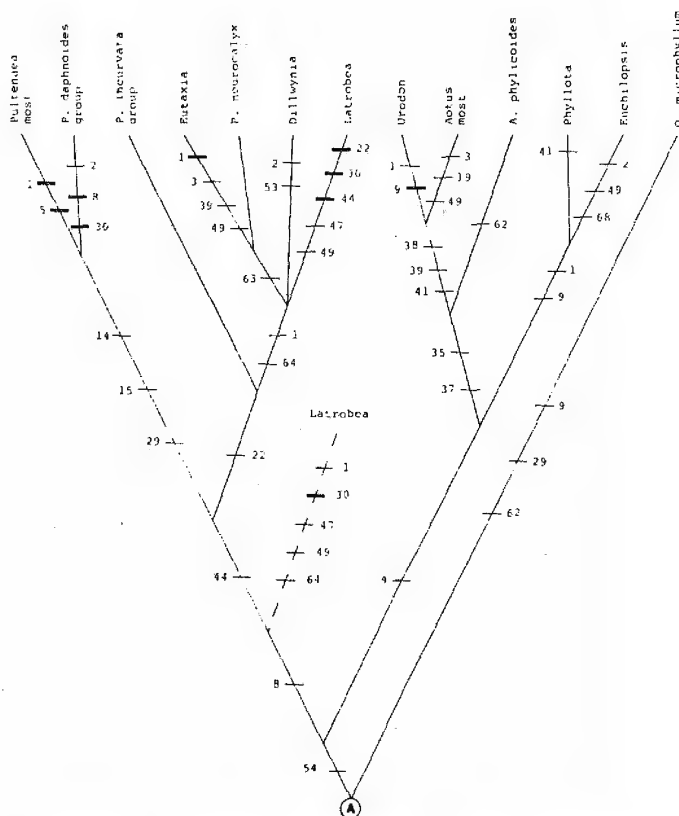


Figure 4 Segment A of the preferred cladogram of the Mirbelieae

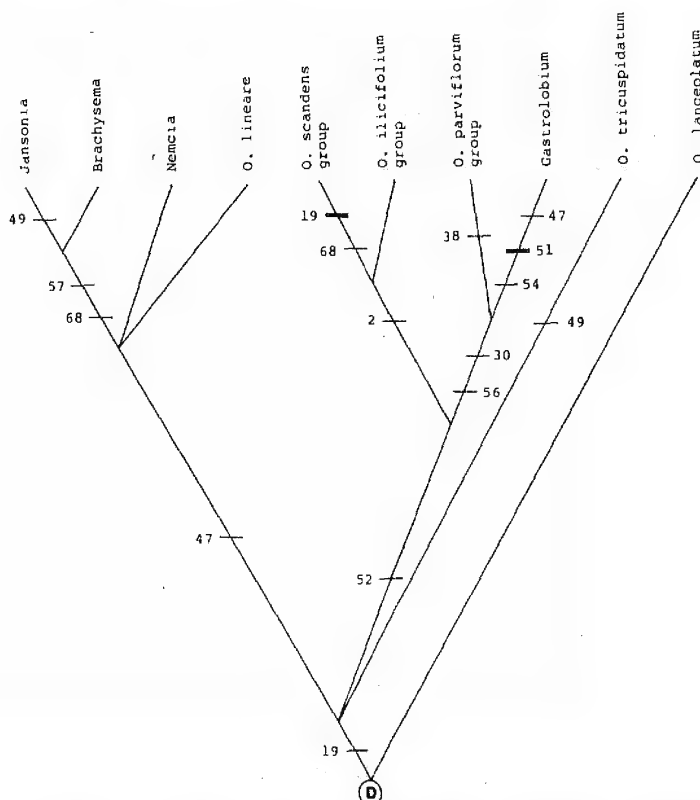


Figure 5 Segment D of the preferred cladogram of the Mirbelieae

SUMMARY

To reiterate - it's important to remember that cladograms resulting from cladistic analyses are working hypotheses which must be evaluated in light of the evidence they present. The relationship between cladograms and the classification has been discussed at length by various authors, (e.g. Wiley, 1981; Nelson and Platnick, 1981; Eldredge and Cracraft, 1980). 'Cladists' believe that only postulated clades should be recognised as taxa and some even maintain that the classifications should mirror precisely the structure of the cladogram on which they are based. I think the cladogram has to be treated simply for what it is - i.e. an hypothesis. We must assess biologically the postulations it suggests. It must be evaluated in terms of the character transformations involved and what they mean in terms of evolutionary or genetic change. There may be genetic quantum leaps in some character state changes and in others a significant but small evolutionary change.

As a method of pattern and character analysis cladistics provides us with the methodology and the techniques by which to delimit natural groups. Compared with other methods there are greater possibilities for the reconstruction of phylogeny of plant groups. Besides the essential criterion of presenting natural groups, most systematists are striving for their classification to have predictivity and to suggest sound groups for further investigation, whether for (e.g.) molecular or chemical analysis or for biogeographic and ecological work. The few examples discussed here suggest that the cladistic groups give greater resolution.

Wiley (1981) pointed out that a good classification should be minimally redundant, minimally novel and maximally informative. Our work should aim to develop classifications that recognise monophyletic groups, but disrupt the present classification (and often the nomenclature) as little as possible.

ACKNOWLEDGEMENTS

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GEOGRAPHIC RANGE AND THE GENUS CONCEPT

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In the planning of the Boden Conference, it seemed to me that some attention should be given to the geography of genera, and perhaps to their ages: whether, for example, there was any predominant geographic pattern which might reflect the framework in which genera are conceived and circumscribed. A brief survey of the literature, however, indicated that little attention has been given to geographic range as a factor in the formulation of the concept of genus. The simple approach I adopted, therefore, was to try to determine the proportion of genera which occur in more than one of the great floristic provinces of the world. Given our present level of knowledge of plate tectonics, we should be able to estimate minimum ages of some genera which have intercontinental distributions. This might establish some sort of time frame in which botanists see the origins and flourishing of genera as usually occurring.

The data summarized below have been extracted from the analyses made by Thorne (1972a, 1972b). Whilst these data may now be partly out of date with respect to current taxonomy, they are probably adequate for the present purpose. In a sense, the data are being used with a purpose opposite to that of Thorne; he studied generic distributions to test biogeographic hypotheses, while here geographic distributions are used to test generic concepts.

Thorne classified intercontinental disjunctions into a number of major types, and determined the number and proportion of genera which showed each disjunction type. In total he scored nearly 3000 genera as having intercontinental disjunctions, although some of these represent relatively small distribution gaps, for example between Australia and New Zealand (48 genera), and between Australia and New Caledonia (19 genera). Other disjunctions scored within this total do not involve substantial ocean gaps, for example between Asia and Malesia/Papuasias (200 genera), and between Asia and Australia (62 genera). The major generic disjunction groups are summarized in Table 1.

The total number of major generic disjunctions recorded by Thorne seems to be very substantial. However it is necessary to consider the data on a relative basis. If the total number of seed plant genera is taken as 12,500, then in global terms only 24% of genera show disjunctions between two or more floristic provinces. Furthermore this statistic of 24% includes small disjunctions such as Alaska-Siberia and Borneo-New Guinea. In fact the 24% fraction comprises c. 5% which show wide disjunctions to several zones, c. 11% which show major disjunctions to two zones, and c. 8% which show smaller disjunctions.

Table 1. Numbers of genera showing selected major geographical disjunctions

| Disjunction Type | | Number of Genera |
|---------------------------------|------|------------------|
| Cosmopolitan | | 125 |
| Arctic | | 8 |
| Boreal | | 50 |
| Beringian Boreal | | 9 |
| North Temperate | | 118 |
| Eurasia/Temperate N America | | 43 |
| Asia/Temperate N America | | 127 |
| Transatlantic North Temperate | | 35 |
| South Temperate | | 9 |
| Antarctic | | 0 |
| Pantropical | | 334 * |
| Amphipacific Tropical | | 89 |
| Africa/Eurasia | | 555 |
| [Africa/Mediterranean | 9 | |
| Africa/Arabia | 38 | |
| Africa/Asia | 200 | |
| Africa/Malesia | 106 | |
| Africa/Australia-New Zealand | 96] | |
| Madagascar/Eurasia | | 47 |
| Africa/South America | | 111 |
| N America/S America | | 7360 |
| [Tropical | 150+ | |
| Temperate | 65+ | |
| Bipolar | 12] | |
| Australia/Africa (Indian Ocean) | | 18 |
| Asia/Pacific | | 460 |
| [Asia/Malesia-Papuasias | 200 | |
| Asia/W Pacific | 130 | |
| Asia/Further Pacific | 40 | |
| Asia/Australia | 62 | |
| Asia/Australia-New Zealand | 6 | |
| Asia/Australia-New Caledonia | 23] | |
| Asia/Temperate S America | | 1 |
| Pacific (within the region) | | 370 |
| [Australia/New Zealand | 48 | |
| W Malesia/E Malesia | 44 | |
| Malesia/Pacific | 43 | |
| Australia/New Caledonia | 19] | |

* includes 103 genera not recorded in Australia

A better indication of the level of major disjunctions within genera may be found in Thorne's study of transatlantic distributions. Of the 111 genera shared only between Africa and South America, 74 are shared only between tropical Africa and tropical America. The total numbers of genera endemic in tropical Africa and tropical America are c. 1000 and 3000 respectively. Thus only 1.8% of the genera confined to

these two tropical areas combined occur in both of them. Furthermore most of the disjunct genera have unbalanced distributions, with most species occurring on one continent and just one or a few on the other. There are very few genera with such significant occurrences in both regions that one must argue a long history of establishment and speciation.

Many of the disjunct genera are pioneers or aquatics, or genera with high dispersibility, and/or show the asymmetry described above. Thus the percentage of genera with presumed ancient establishment and significant speciation in two or more widely disjunct areas is quite low. Thus genera like our old southern hemisphere favourite Nothofagus are rather exceptional.

It would be unwise to attempt to draw too much from this analysis. However it appears that the great majority of genera are younger than the major phases of plate movement. Or conversely, in any taxon which shows ancient establishment and diversification in two or more areas which have been physically isolated for a long time, then some special environmental or genetic conditions must be involved if our judgement tells us that they are best treated as constituting a natural genus.

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Chemical Characters and Generic Delimitation

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The use of chemical characters in systematics is known as chemotaxonomy, or biochemical systematics. As a distinct discipline, it dates back to the early 1960's. In this and other respects it has much in common with numerical taxonomy, the main difference being that chemotaxonomy is a source of new data, whereas numerical taxonomy is a way of analysing existing data. Both were brought together as distinct disciplines by the publication of books in 1963 - *Principles of Numerical Taxonomy* by Sokal and Sneath on the one hand, and *Biochemical Systematics* by Alston and Turner on the other. Some proponents of each saw their discipline as the answer to problems in taxonomy; this is not unlike the situation with cytotaxonomy or experimental taxonomy a generation earlier, or cladistics a generation later. These new disciplines were going to be the only way to do taxonomy, and would provide solutions to vexing problems such as generic delimitation. Of course, none of these disciplines ever did provide all the answers, and no one ever will. Rather, each is now seen as one of a number of useful approaches that should be employed in any detailed study.

Before discussing some examples of the utility of chemical characters in generic delimitation, there are some general points that should be made. Most of the chemical information available on plants has been gained by chemists and, while this adds to our general knowledge of plants, it has rarely been collected in a manner that allows any taxonomic conclusions to be drawn. Generally it is only when a botanist undertakes a chemotaxonomic study personally, or collaborates directly with a chemist, that sufficient information is collected in a systematic manner, thus allowing taxonomic conclusions to be drawn.

There have been very few studies involving problems of generic delimitation where a set of chemical characters has been studied fully throughout all the species involved. The main reason for this is the time involved in determining the appropriate chemical composition of the large number of populations and species within the study. In this respect, chemical characters are similar to other characters in which there is a fair amount of work involved in studying each sample, for example anatomical and ultrastructural characters. In these situations, after establishing the variability of the characters concerned, some sampling regime has to be set up involving the species or species groups within the area of the study. Following this introduction, some examples of the use of chemical characters in generic delimitation will be discussed, where possible drawing examples from the Australian flora.

Lemnaceae

One of the more convincing examples was in fact one of the first, the work of McClure and Alston (1966) on the Lemnaceae. The Lemnaceae was treated, at that time at least, as consisting of four well-defined genera - Spirodela, Lemna, Wolffia and Wolffiella. The family shows extreme morphological reduction, both in the vegetative and in the floral parts, such that there are few morphological characters available for use in classification.

McClure and Alston studied 22 of the then recognized 29 species, representing all four genera, for flavonoids. A number of interesting points emerged and, as regards generic delimitation, there are two worthy of mention.

The first relates to Spirodela oligorhiza. This is somewhat intermediate, morphologically, between Spirodela and Lemna, and is placed somewhat uncertainly in Spirodela. As regards its flavonoid composition, this species shows some compounds in common with the other species of Spirodela, and some compounds in common with the species of Lemna, particularly Lemna minor. This indicates a closer relationship between Spirodela oligorhiza and Lemna minor than was generally realised, but it does not solve the initial problems, but rather only highlights them. The generic placement of the species oligorhiza, and the relative status of Spirodela and Lemna remain unresolved.

The second point relates to the genera Wolffia and Wolffiella. There had been some indecision, on morphological grounds, as to whether Wolffia and Wolffiella were two separate genera. The flavonoid data indicate that Wolffiella is a group of closely related species, for the most part distinct from Wolffia. Of more interest is the situation in Wolffia. Here there are two quite distinct groups of species, one showing relationships more with Wolffiella, and the other more with Lemna. Thus the chemical evidence indicates that Wolffia, as then constituted, is a markedly polyphyletic genus, and should be split. It also provides insights into the relationships and possible phylogeny of these groups.

Malus and Pyrus (Rosaceae)

It is now generally recognized that the apples and pears belong to separate genera, Malus and Pyrus respectively. However they have not always been separated in this way, and the morphological characters separating the two groups are minor, and relatively few in number. Chemically, however, the two groups are quite distinct as regards their flavonoid composition. In a study of all known species of the two groups, Challice (1974) showed that Malus produces dihydrochalcones as the major leaf flavonoids, whereas these are completely absent from Pyrus, which produces the simple phenolic arbutin as the major leaf flavonoid. There are also a number of differences in the minor leaf flavonoids of the two groups.

Restionaceae

This family has about 30 genera and 400 species, with a basically southern hemisphere distribution, centred in Australia and Southern Africa. Generic delimitation in the family has proved difficult, in part at least because of their almost leafless habit and the fact that many species are dioecious.

Based on morphological characters, three genera (Hypolaena, Leptocarpus and Restio) were believed to occur both in Australia and Southern Africa. In an anatomical survey of the family, Cutler (1969) concluded that the Southern African species and genera were more closely related to one another than any were to the Australian species and genera, and vice versa. Thus there are two distinct groups of species, one basically Australian and the other basically Southern African.

In a limited survey of 33 South African species and 14 Australasian species, Harborne (1979) showed that the flavonoid data correlated with the anatomical data in distinguishing these two basic groups. Thus these data (anatomical and chemical) indicate a single original division of the family within Gondwanaland into a Southern African line and an Australasian line. The links between Australia and South America and Australasia and Malesia are seen as much more recent.

Although these results have not been incorporated as yet into the formal taxonomy of the family, they are generally recognised, for example by Johnson and Briggs (1981, 1983) who indicate that there is further evidence to support them.

Dacrydium s.l. (Podocarpaceae)

It has been recognised for some time that Dacrydium is a markedly heterogeneous group. Quinn and Gadek (1981) surveyed the biflavonyls of twelve species, which represented all the species groups within the genus. Their survey distinguished five basic groups within Dacrydium s.l. Together with a re-examination of ovule orientation (Quinn, 1982), this led to the delimitation of five distinct genera.

Utility of flavonoids

So far, all of the examples discussed have used flavonoids as the chemical characters. This is a reflection of the fact that these compounds are in general more useful at the generic level than are many other compounds. There are probably three main reasons for this:

- (i) empirically it is found that, in general, flavonoids tend to be relatively constant within a species, but often show differences between sections, subgenera or genera;
- (ii) flavonoids are stable compounds, and it is relatively easy to determine the flavonoid composition of a plant using fairly

simple techniques;

- (iii) often only relatively small amounts of dried leaf material are needed, and it is even possible to use herbarium material in surveys if necessary.

This is not to say that other compounds may not prove useful at times in generic delimitation, although they often do not show all three advantages noted above. Brief mention will be made of examples where some of these other compounds have proved useful at this level.

Terpenoids

The lower terpenoids, which are major components of the volatile oils or essential oils of plants, have often proved useful at and around the species level in gymnosperms, and in studies of variation within species of Eucalyptus, but would appear to have little or no use at higher levels.

There are cases, however, where they may prove useful. Thus in the Dipterocarpaceae, Dipterocarpus appears to differ in its sesquiterpene pattern from Doona (Bisset et al. 1966). In the Apiaceae, various genera in the tribe Caucalideae show differences in the volatile oils of their fruits (Williams and Harborne 1972), and there may be useful tribal differences as well (Adcock and Betts 1974).

In the higher molecular weight non-volatile terpenoids, the triterpenoids may prove useful again in the Dipterocarpaceae (Bisset et al. 1966, Bandanarayake et al. 1977).

Non-protein amino acids

These have proved useful in a number of cases, mostly involving the non-protein amino acids of seeds in the Leguminales. Early studies of non-protein amino acids in Lathyrus and Vicia by Bell (1966) gave valuable insights into the distinction of these two genera, and indicated possible lines of evolution within them. Similar studies also proved useful in the genera Phaseolus and Vigna.

There has also been some interesting work on the non-protein amino acids in Acacia. The amino acids in the seeds of over 100 species have been studied (Seneviratne and Fowden 1968, Evans et al. 1977), and very clear cut correlations between amino acid content and series and sectional classification have been found.

Alkanes

The alkane hydrocarbons have rarely proved useful at the generic level, although Scora et al. (1975) found that the pattern of alkanes in taxa of Persea (Lauraceae) was very different from that in the one species studied of the related genus Beilschmiedia.

Flavonoids and Phylogeny

For a concluding section, some examples are discussed where flavonoids have provided useful or interesting data on the systematic position or evolutionary relationships of some Australian genera.

Idiospermum

Idiospermum australiense constitutes a monotypic genus of north eastern Australia. It was originally placed in the Calycanthaceae, but is now generally placed in its own family, the Idiospermaceae. A study of the flavonoids of Idiospermum, and of Calycanthus and Chimonanthus from the Calycanthaceae, revealed marked differences (Sterner and Young 1980), thus supporting the morphological and anatomical data in separating

Idiospermum to its own family.

Eupomatia

The genus Eupomatia contains two species of eastern Australia and New Guinea. It was originally placed in the Annonaceae, but is now recognised as a distinct family, whose relationships are not clear. Comparison of the flavonoids of the Eupomatiaceae with those of a number of families of the Magnoliales indicated a possible relationship with the Winteraceae (Young 1983).

Blepharocarya

The genus Blepharocarya, with two species in northern Australia, was originally described in the Sapindaceae, but is now generally placed in its own family, the Blepharocaryaceae. A study of the biflavonyls of the two species indicates an affinity of the family with the Anacardiaceae (Wannan et al. 1985).

Conclusion

Recent advances in systematics have led to a greater understanding of the concept of a genus. To put that concept into practice is the field of generic delimitation. That this is not easy is evidenced by the conflicting views relating to genera to be found in a number of cases. Hopefully, the present review indicates that whenever there is a major study of generic limits within a group, chemical characters have much to offer.

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POLLINATION SYNDROMES AS GENERIC DETERMINANTS

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RESUME

It is a delusion to seek to find "good generic characters", since there are none and it is a misconception to consider one type of taxonomic character superior to another since no one type of character provides more reliable insights into patterns of common ancestry. This reality is as true for floral morphological characters, or pollination syndromes, as it is for any character type!

FLORAL SYNDROMES

Flowering-plant taxonomists traditionally place a heavy reliance on floral characters in assessing relationships and in arriving at taxonomic conclusions. This tradition can be traced back to the publication of 'Genera Plantarum' in 1737, in which Linnaeus evoked an artificial 'sexual system', based on floral characters, to define his classes and orders. Remarkably, the great majority of Linnaeus's genera and subordinate taxa have survived to form the core of all subsequent systems of classification.

Historically, floral characters have been used in taxonomy primarily because of the rich supply of variables that they provide. Unfortunately, taxonomists generally have not been aware of the adaptive significance of the floral characters that they use to construct their classifications and this has led, on occasions, to serious misinterpretations of homology.

Numerous correlations exist in most flowers between colour, scent, form, texture, and the recognized behaviour patterns of the predominant pollinators. Such correlations have been grouped into floral syndromes, or pollination syndromes, and a table of these for animal-pollinated plants is presented in Table 1.

Grant (1949) illustrated the relative taxonomic importance of floral characters as correlated with mode of pollination (Figure 1). Flowering plants pollinated 'promiscuously' by wind, water, or unspecialized insects tend to be incapable of developing barriers to interspecific pollination - these 'promiscuous' angiosperms are separated taxonomically more by non-floral characters such as fruit or vegetative characters. Floral isolating mechanisms tend to be confined to those groups of angiosperms possessed of flowers sufficiently complex to ensure their 'non-promiscuous' pollinations - these 'non-promiscuous' angiosperms are separated taxonomically by floral characters that serve as barriers to un-specialized pollen vectors.

A review of angiosperms as a whole shows that every morphological character that is used to distinguish families and orders can, in some groups, vary at the level of genera and species - note how the floral morphological characters in Table 2 are diagnostic at various hierarchical levels! Stebbins (1977) argues that this type of variation is the result of evolutionary canalization, i.e. the way in which a population will respond adaptively to a changing environment depends to a large degree upon the adaptations that it has already acquired as a result of previous adaptive radiations. Colin Webb talks more about this concept in his paper on breeding systems.

An appraisal of the significance of pollination systems in evolution may be made by analyzing the different kinds of systems present in a plant family, as well as their proportions, and the circumstances in which they are found. Since this has been done for the Rutaceae (Armstrong 1979, 1983), we can examine the significance of bird pollination in the circumscription of higher taxa in the Boronieae, a tribe noted for the diversity of its floral morphological types.

THE SYNDROME OF ORNITHOPHILY IN THE RUTACEAE

Bird pollination (ornithophily) exemplifies a very specialized pollination syndrome in which the highly modified floral characters can serve as effective barriers to interspecific pollination. In the Rutaceae, bird pollination is a conspicuous floral syndrome and is a relatively common feature, particularly in the Australasian tribe Boronieae.

Engler's (1896) classification of the Boronieae saw the tribe divided into 5 sub-tribes, based primarily on the distribution of floral morphological characters:

- Boroniinae: spreading free petals, non ligular stamens and opposite leaves (7 genera).
- Correinae: petals fused, and non ligular stamens (1 genus).
- Diplolaeninae: flowers in dense terminal clusters surrounded by an involucre of bracts, non ligular stamens (1 genus).
- Eriostemonieae: spreading free petals, non ligular stamens and alternate simple leaves (9 genera).
- Nematolepidinae: stamens with a ligular structure at their base (4 genera)

An examination of the pollination spectrum of the Boronieae reveals that entomophily (insect pollination) is the most widespread

| Syndrome | Pollinators | Anthesis | Colors | Odors | Flower shapes | Flower depth | Nectar guides | Rewards |
|-----------------|------------------------|--------------------------|-----------------------------|-----------------------------------|---|---------------------------------|---------------|--|
| Cantharophily | Beetles | Day and night | Variable, usually dull | Strong, fruity or aminoid | Actinomorphic | Flat to bowl-shaped | None | Pollen or food bodies |
| Sapromyophily | Carion and dung flies | Day and night | Purple-brown or greenish | Strong, often of decaying protein | Usually actinomorphic | None, or deep if traps involved | None | None |
| Myophily | Syrphids and bee flies | Day and night | Variable | Variable | Usually actinomorphic | None to moderate | None | None or pollen or nectar |
| Melitophily | Bees | Day and night or diurnal | Variable but no pure red | Present, usually sweet | Actinomorphic or zygomorphic | None to moderate | Present | Nectar (41.6%) and pollen; open or concealed |
| Sphingophily | Hawkmoths | Nocturnal or crepuscular | White or pale to green | Strong, usually sweet | Actinomorphic; held horizontal or pendant | Deep, narrow tube or spur | None | Ample nectar (22.1%); concealed |
| Phalaenophily | Small moths | Nocturnal or crepuscular | White or pale to green | Moderately strong, sweet | Actinomorphic; held horizontal or pendant | Moderately deep tube | None | Nectar; concealed |
| Psychophily | Butterflies | Day and night or diurnal | Bright red, yellow, or blue | Moderately strong, sweet | Usually actinomorphic; upright | Deep narrow tube or spur | Present | Nectar (22.8%); concealed |
| Ornithophily | Birds | Diurnal | Bright red | None | Actinomorphic or zygomorphic | Deep, wide tube or spur | None | Ample nectar (25.4%); concealed |
| Chiropterophily | Bats | Nocturnal | Dull white or green | Strong, fermented | Actinomorphic or zygomorphic | Brush- or bowl-shaped | None | Ample nectar (18.9%) and ample pollen; open |

Table 1. Floral syndromes of animal-pollinated plants. (From Wyatt 1983).

| Character difference | Diagnostic at species level | Diagnostic at genus level | Diagnostic at family or order level |
|---|---|--|--|
| Woody vs. herbaceous growth habit | <i>Mimulus longiflorus</i> vs. <i>M. clelandii</i> | <i>Zanthorhiza</i> vs. <i>Coptis</i> (Ranunculaceae) | Myrsinaceae vs. Primulaceae |
| Compound vs. simple leaves | <i>Ranunculus repens</i> vs. <i>R. cymbalaria</i> | <i>Eschscholtzia</i> vs. <i>Dendromecon</i> (Papaveraceae) | Oxalidaceae vs. Linaceae |
| Capitate vs. umbellate or other kind of inflorescence | <i>Arenaria congesta</i> vs. <i>A. maradenia</i> | <i>Trifolium</i> vs. <i>Melilotus</i> (Leguminosae) | Dipsacaceae vs. Valerianaceae; Asterales (Compositae) vs. Campanulales |
| Bilateral (zygomorphic) vs. radial (actinomorphic) | <i>Saxifraga sarmentosa</i> vs. other <i>Saxifraga</i> spp. | <i>Tolmiea</i> vs. <i>Heuchera</i> (Saxifragaceae) | Violaceae vs. Cistaceae |
| Foliaceous vs. awnlike or pappuslike calyx lobes | <i>Marrubium Alysson</i> vs. <i>M. vulgare</i> | <i>Dracopcephalum</i> vs. <i>Galeopsis</i> (Labiatae) | Dipsacaceae vs. Caprifoliaceae; Asterales vs. Campanulales |
| Tetramerous vs. pentamerous perianth | <i>Rhamnus crocea</i> vs. <i>R. californica</i> | <i>Ludvigia</i> vs. <i>Jussiaea</i> (Onagraceae) | Cruciferae vs. Moringaceae |
| Corolla lobes separate vs. united | <i>Crassula Zeyheriana</i> vs. <i>C. glomerata</i> | <i>Monotropa</i> vs. <i>Pterospora</i> (Monotropaceae) | Pyrolaceae vs. Ericaceae |
| Perianth biseriate vs. uniseriate | <i>Sagina nodosa</i> vs. <i>S. decumbens</i> | <i>Agrimonia</i> vs. <i>Sanguisorba</i> (Rosaceae) | Portulacaceae vs. Chenopodiaceae |
| Carpels separate vs. united | <i>Saxifraga Lyallii</i> vs. <i>S. arguta</i> | <i>Delphinium</i> vs. <i>Nigella</i> | Dilleniaceae vs. Actinidiaceae |
| Ovary superior (hypogynous) vs. inferior (epigynous) | <i>Saxifraga umbrosa</i> vs. <i>S. caespitosa</i> | <i>Tetraplasandra</i> vs. other Araliaceae | Loganiaceae vs. Rubiaceae |
| Placentae axial vs. parietal | <i>Hypericum perforatum</i> vs. <i>H. anagalloides</i> | <i>Boykinia</i> vs. <i>Heuchera</i> (Saxifragaceae) | Theaceae vs. Cistaceae |
| Ovules numerous vs. solitary | <i>Medicago sativa</i> vs. <i>M. lupulina</i> | <i>Spiraea</i> vs. <i>Holodiscus</i> (Rosaceae) | Campanulales vs. Asterales |

Table 2. Distribution of character differences at various hierarchial levels. (From Stebbins, 1977)

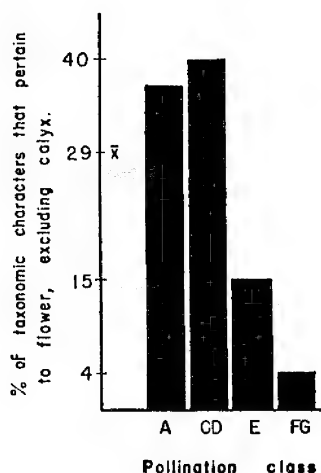


Figure 1. The relative taxonomic importance of floral characters (excluding those of calyx, fruit and seeds), as correlated with mode of pollination in Angiosperms. "A": Bird-pollinated plants. "CD": Bee and long-tongued fly plants. "E": Plants Pollinated promiscuously by unspecialised insects. "FG": Wind and water-pollinated plants. "x": Mean of all classes. (From Grant, 1949).

system occurring in 74% of genera (17/23) and 88% of species (232/264). Ornithophily is characteristic of 39% of genera (9/23) and 12% of species (31/264). All genera known to have bird pollinated taxa are highlighted (*) in Figure 2. Bird pollination is rare in *Eriostemon* (9%, 3/33 spp.) and *Phebalium* (9%; 4/45 spp.), predominant in *Correa* (91%; 10/11 spp.), *Diplolaena* (all 6 spp.) and *Drummondita* (all 4 spp.), and characteristic of the monotypic genera *Chorilaena*, *Nematolepis*, *Muiriantha* and *Rhadinothamnus*. All bird-pollinated species are characterized by green or red-orange blossoms, the colour frequently being borne by the stamens rather than the petals.

Recent cladistic studies in *Boroniaceae* (Armstrong, 1984), reveal that the various floral adaptations that have evolved to facilitate nectar-seeking birds, have arisen independently on numerous occasions in this tribe (Figure 2). The analysis suggests that the syndrome of bird pollination is homoplasious (a parallelism¹), having arisen independently from insect-pollinated ancestors on at least seven separate occasions during the tribe's evolutionary history.

The ligular structures present in *Chorilaena*, *Nematolepis*, *Muiriantha* and *Rhadinothamnus*, are adaptations to retain, within the blossom, the large volumes of nectar produced in these pendant-flowered taxa - this nectar retaining function is performed in other pendant, bird-pollinated blossoms by the strategic placement of hairs on the adaxial face of the staminal filaments (eg. *Diplolaena*), or by the major modification of the filament's shape (eg. *Correa*). It appears likely that the ligular structures evolved from the filaments of insect-pollinated ancestors, following modification of the staminal morphology, to produce a flap like outgrowth on the filament's adaxial surface.

A more detailed examination of the cladogram (Figure 2) reveals the questionable status of the ligule-bearing, "genera" of the *Boroniaceae*. By way of example, the bird-pollinated "genus" *Nematolepis* is shown to form a monophyletic assemblage with the insect-pollinated taxon '*Phebalium* section *Eriostemoides*'. The blossom morphology of the ancestor of this assemblage probably resembled that found in some of the extant taxa of *P.* sect. *Eriostemoides*. Evolution of the bird pollination syndrome within the assemblage, involved the following pathways of adaptive radiation:

- Inflorescence multi-branched and many-flowered, to inflorescences unbranched and flowers solitary;
1. Parallelism is the independent development of similar apomorphies from the same plesiomorphic state (Bremer and Wanntorp 1978).

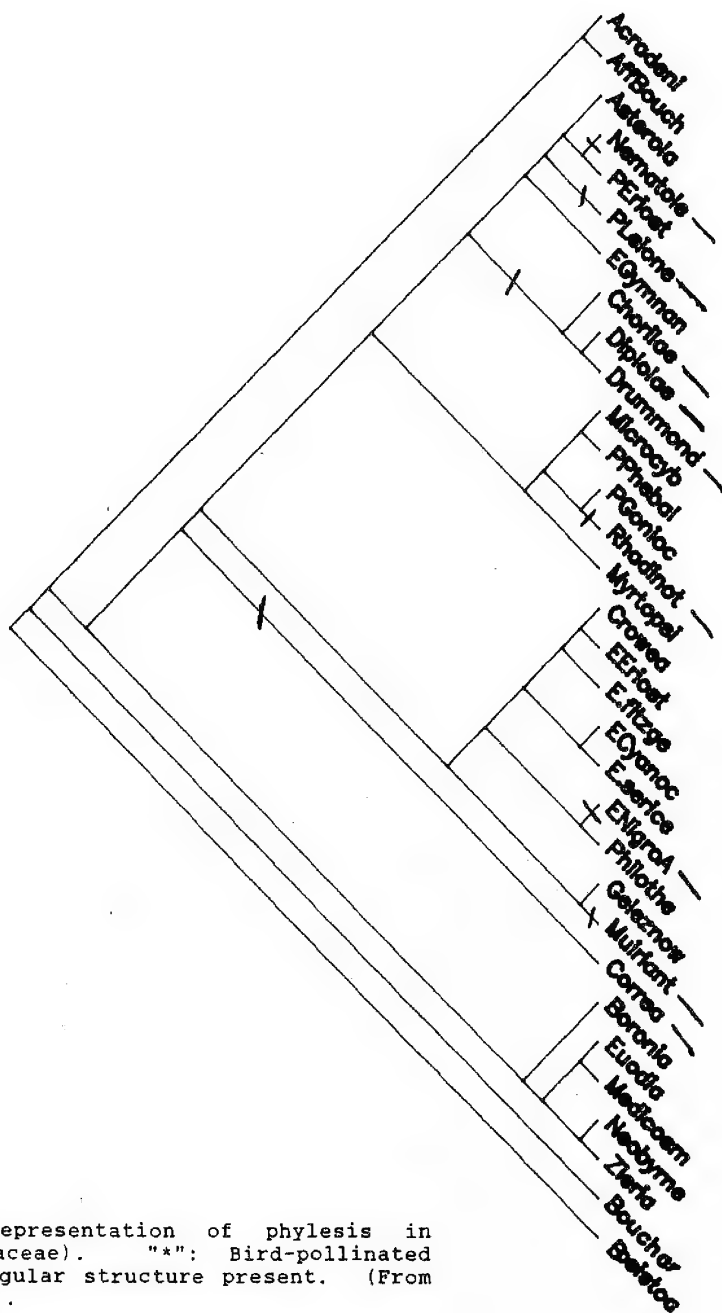


Figure 2. A cladistic representation of phyletic in Boronieae (Rutaceae). "*" : Bird-pollinated taxa. "-" : Ligular structure present. (From Armstrong, 1984).

- . Flowers upright, to flowers pendent;
- . Petals free and spreading, to petals united and tubular;
- . Nectary small, to nectary conspicuous and producing large quantities of nectar;
- . Filaments sparsely ciliate in lower half, to filaments with a short hirsute ligule above the base.

The cladistic analysis suggests that the "ligule" has arisen on at least four separate occasions in the Boronieae and hence, this "character" is homoplaseous and non-homologous. It was Engler's use of non-homologous floral characters that led to the circumscription of artificial taxa within the tribe. Such phenetically defined groups have little, if any, biological relevance!

SUMMARY

Pollination syndromes, defined by floral morphological characters, have no greater capacity to circumscribe higher taxonomic categories than any other character type. Angiosperm taxonomy is replete with examples of monotypic genera defined by unique or unusual floral characters, but such constructions are rarely found to be phylogenetically informative.

Generic rank is not an objective reality (Stevens 1985). To be informative, genera need to be phylogenetically based and strictly monophyletic. Classifications that are congruent with the best available hypothesis of phylogeny, are of the greatest relevance to biologists.

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BREEDING SYSTEMS AS GENERIC DETERMINANTS

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Reproductive characters are usually considered to be relatively conservative and are therefore often used to define taxa above the level of species. This paper firstly presents some ideas about how characters might be assessed as to their usefulness in taxonomy, then considers the breeding system itself as a character, and finally provides some examples of how an understanding of the breeding system may help in evaluating particular reproductive characters.

PHYLOGENETIC CONSTRAINT AND THE ASSESSMENT OF CHARACTERS

Phylogenetic constraint may be defined as the way in which the evolutionary history of a taxon influences the ease with which particular characters can respond to selection (Webb 1984). For example, ovule number and stamen number are almost invariably constrained at 2 and 5 respectively in Apiaceae, stamen number is constrained at 5 while ovule number is highly variable among species of Gentiana, and in Ranunculus both characters are very labile. Thus these two characters might be used by taxonomists at different levels in the three families.

Four types of information might be useful when trying to decide the taxonomic value of a reproductive character. Firstly, the usefulness of a character may be indicated by the number of times it has independently evolved in that family or in closely allied families (its level of constraint). Secondly, an understanding of the genetic basis of the character may help - character states which are the result of single gene differences are not likely to be useful although they may appear quite striking. Thirdly, it is important to understand the functional significance of structures associated with pollination and dispersal - in other words the selective advantage of each of the alternative character states. Fourthly, an understanding of what might be called the ecological context may help - that is, an understanding of why certain reproductive characteristics, such as fleshy fruit and dioecism, are often associated or why some sexual systems are frequent in particular areas or habitats. This can often be appreciated by looking at parallel developments in unrelated families.

THE BREEDING SYSTEM AS A GENERIC CHARACTER

The breeding system has long been used as a character in plant taxonomy. In his sexual system of classification, Linnaeus (1754) had classes Monoecia, Dioecia and Polygamia. In the dioecious class, for example, were included an assortment of unrelated genera such as Salix, Myrica, Cannabis, Mercurialis, Carica and Juniperus - but these classes were not supposed to be natural.

In natural systems of classification too, the breeding system has been a useful character. Consider firstly sexual dimorphism, where separate plants are specialized as seed or pollen parents. In a few cases sexual dimorphism, particularly dioecism, is one of the characters used to define families, as for example with Salicaceae, Pandanaceae and Garryaceae. At generic level it may also be useful. In a group of 5 related genera of Apiaceae in Australasia, 2 genera (Aciphylla and Anisotome) are dioecious, while the other 3 (Gingidia, Lignocarpa and Scandia) are basically gynodioecious (Webb 1979). [In gynodioecious species female plants are completely pollen sterile, but male plants produce a significant amount of seed as well as pollen.] Other characters associated with the breeding system are also useful in these genera. In female plants of Aciphylla and Anisotome stamens are reduced to macroscopic staminodes, whereas in the other 3 genera staminodes are rudimentary. Also females of both species of Lignocarpa are distinguished from those of other genera in that they have no visible petals.

There are several examples where sexual dimorphism characterizes only part of a genus, as in Ficus (Hill 1967), or where this form of breeding system appears to be unhelpful to the taxonomist. Many genera contain both sexually dimorphic and cosexual species - Fragaria, Potentilla, Hebe, Hydrocotyle, Fuchsia, Gunnera, Cotula, Solanum and Urtica to name a few. In the grasses, on the other hand, dioecism defines several genera in the Paniceae (H.E. Connor, pers. comm.).

Monoecism, andromonoecism and gynomoecism have all been used as generic characters. Again in the grasses, in tribe Paniceae monoecism (separate male and female flowers on the same plant) defines quite a number of genera (H.E. Connor, pers. comm.). Maybe this is because grass

taxonomists have so few characters to work with that they have looked at flowers more carefully. In Asteraceae there are many examples where the male or female fertility of outer or inner florets is a useful character. For example in Cotula, sects. Strongylosperma and Cotula are with very few exceptions composed of species with hermaphrodite central florets while in sect. Leptinella the central florets are male or the species are dioecious (Lloyd 1972). Similarly, in the related genus Soliva the capitula are monoecious with outer florets female and inner male. In the Senecioneae, one of the characters which separates Traversia from Brachyglottis is that the outer florets are hermaphrodite rather than female (Nordenstam 1978).

Dichogamy, the temporal separation of pollen and stigma presentation, has been little used as a character by taxonomists, although there are indications that it may be useful. The two main classes of dichogamy, protandry and protogyny, are not randomly distributed among angiosperm families - protandry is very often part of the breeding system in Apiaceae, whereas protogyny is common among "primitive" angiosperms. Duodichogamy, in which all inflorescences on a plant go through more or less synchronous male, female and finally male phases, is common in Sapindaceae, Aceraceae and Hippocastinaceae (Lloyd and Webb 1986). On the other hand, protandry and protogyny may sometimes be found in one genus, as for example in Ranunculus, Hebe and Uncinia (Godley 1979).

Herkogamy, the spatial separation of pollen and stigma presentation, shows few trends which would be useful in classification except in its most specialized forms such as sensitive stigmas (Webb and Lloyd 1986). Heterostyly, a form of reciprocal herkogamy, is confined to very few families, but almost always occurs in genera along with homomorphic species. It is nevertheless useful as a character to separate Jepsonia from other genera of the Saxifragaceae (Ornduff 1969). Neither selfing versus outcrossing, nor self compatibility versus self incompatibility are of much if any use as generic characters. Self compatible and self pollinated taxa are frequently closely related to outcrossing taxa and selfing may evolve independently many times in one plant group. In Onagraceae Raven (1979) has estimated that self pollination has evolved independently at least 150 times.

Accurate quantitative descriptions of breeding systems enhance their usefulness as characters. In many early taxonomic works, sexually dimorphic plants were described by loosely defined terms such as polygamy or polygamo-dioecy. It is essential that descriptions of plant breeding systems be based on field observations so that different morphs which co-occur can be distinguished and described.

Accurate descriptions of breeding systems may also help to establish relationships between genera by giving an indication of the evolution of the breeding system, and so help to determine character polarity. In the sexually dimorphic genera of the Apiaceae discussed above, the occasional inconstancies on male plants of the dioecious genera Aciphylla and Anisotome indicate an affinity with the gynodioecious genera. If the inconstancies in the dioecious genera suggested a monoecious rather than a gynodioecious pathway from hermaphroditism to dioecism - a few female flowers on male plants and a few male flowers on female plants - then the dioecious genera could not be considered close to the gynodioecious ones.

The two main pathways to dioecism are via gynodioecism and monoecism, but dioecism may also arise from heterostyly (Lloyd 1980). In families in which heterostyly occurs, for example Rubiaceae, dioecious genera may be closely related to genera with heterostylous species. This is probably not the case with Coprosma, but this genus nevertheless provides an interesting example. The genus is basically dioecious but one recently described species in New Zealand, C. talbrockiei, has solitary, terminal, hermaphrodite flowers (Moore and Mason 1974), whereas inconsistencies in Coprosma indicate evolution from hermaphroditism via monoecism (Wild and Zotov 1930). This breeding system character alone is not sufficient to exclude this species from the genus, but it is enough to suggest the need for a closer look at other characters important for its classification.

FUNCTIONAL SIGNIFICANCE, ECOLOGICAL CONTEXT AND REPRODUCTIVE CHARACTERS

Both the functional significance of a character and that referred to above as its ecological context need to be kept in mind when assessing generic characters. What follows are examples of cases when ignoring these two factors leads to difficulties in classification.

In the middle of last century John Lindley (1847) commented on the work of Schomburgk, who had described the production on a single spike of flowers of 3 types, referable to 3 different, supposed good orchid genera. The flowers were identified as Monachanthus viridus, Myanthus barbatus and a Catasetum. This observation moved Lindley to comment "...such cases shake the foundation of all our ideas of the stability of genera and species ...". Many species of the Catasetinae are now known to be diphasic - they produce male flowers early in life or in poor sites, and female or hermaphrodite flowers later or when in better sites (cf. Lloyd and Bawa 1984). There are similar examples at species level in other families. In a recent study of Central American Solanum Anderson and Levine (1982) showed that 3 accepted species names actually applied to 3 morphs of a single functionally dioecious species. A similar confusion has occurred in the taxonomy of gynodioecious species of Fuchsia (Breedlove 1969). For the South African flora, Ornduff (1974) noted that 3 species of Oxalis accepted by Jacquin were stylar morphs of a single species, and in Boraginaceae variations in the style length and anther position in heterostylous and homostylous species have been partly responsible for superfluous names (Ornduff 1969). It is rather surprising to find that in Flora Europaea (Tutin 1964) wild plants of the dioecious Ficus carica are still referred to var. caprificus, the name used for male plants when the two sexes were treated as different varieties. These examples stress the need for field studies of populations so that breeding systems are described accurately.

Selfing plants can present particular problems, especially when the flowers are very reduced and autogamous so that many characters present in related xenogamous species are absent (cf. Ornduff 1969, Table 1). The work of Garnock-Jones (1976) on Parahebe provides a good example. He described 2 different pollination systems in P. linifolia - autogamy and entomophily - which occur in different parts of the species range. If the biological significance of the striking difference in the appearance of the flowers in the two types had not been appreciated, the two may have been treated at least as distinct species rather than as subspecies. Autogamy can lead to other taxonomic problems. Where a species is predominantly selfing but occasionally outcrosses, apparently distinct

racess may develop and these may end up being treated as species. This has occurred in Soliva subgen. Soliva where the 4 species usually accepted are no more than self-perpetuating parts of a single variable species. The variation in achene morphology within this Soliva species indicates that some caution is needed when using achene characters to define genera in this part of the Anthemideae.

Transference of function (Stebbins 1974) may also create problems for taxonomists, for example when the ability to form a fleshy disseminule rather than the detail of which floral part becomes fleshy may be the evolutionarily significant character. Thus the distinction between the ericaceous taxa Gaultheria, in which the capsule is often invested by a fleshy calyx, and Pernettya, in which the ovary wall becomes fleshy, may not be as great as it may appear.

Recent work in reproductive biology has described a number of correlations between plant breeding system and other factors such as pollinator type, fruit type and habitat (Bawa 1980, 1982). In such cases parallel trends can often be found in divergent families and the breeding system may not be much use as a generic character. Dioecism, for example, is common on some islands, including New Zealand, and yet this character has been used to separate some New Zealand species as monotypic genera. Tetrapathaea is a monotypic genus separated from Passiflora on the basis of its dioecism and tetramerous flowers. Hutchinson (1967), in treating Tetrapathaea as a synonym of Passiflora, noted the occurrence of dioecism in other genera in New Zealand. Green (1972) retained the New Zealand species in Passiflora but as a distinct subgenus on the basis of the tetramerous flowers and 2 other characters. Oddly, Hutchinson (1969) used dioecism as one character to separate the then monotypic New Zealand Oreoporphantha from Porphantha; the occurrence of dioecism elsewhere in Euphorbiaceae would also argue against this split.

Dioecious plants often have relatively small, simple flowers pollinated by unspecialized pollinators, and these two characters together may give a very different appearance to quite closely related genera. Two woody genera of the Violaceae in New Zealand provide an example. Melicytus is dioecious and has relatively unspecialized flowers; Hymenanthera is hermaphroditic or gynodioecious and has flowers which retain to a greater degree the specialized pollen presentation mechanism of many Violaceae. Powlesland (1984) has described details of and variation in flower morphology among species of Melicytus, which as suggested by Lloyd (1975) clearly indicate that these two genera should be united.

CONCLUSION

Research in reproductive biology, particularly the more theoretical work of the last decade, has provided a framework for understanding plant breeding systems. Theoretical evolutionary models allow accurate prediction of many characters associated with particular breeding systems, but it is important for taxonomists to remember that many such models are not phylogenetically based; rather they describe the action of the same selective pressures in unrelated plant groups. The modes of pollination and dispersal in particular have very obvious effects in plant structures and so a fuller understanding of both will often be important in correctly interpreting reproductive characters.

ACKNOWLEDGMENTS

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THE SYSTEMATIC STATUS OF LARGE GENERA IN THE ASTERACEAE. I.

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In theory "Large Genera" can exist in any large group of plants such as the Asteraceae and they should be recognized by taxonomists. However, in practice, at least in the Asteraceae, "Large Genera" are thoroughly buried among the more numerous large generic concepts that are nothing but monuments to the ignorance and timidity of past taxonomists. The Family Asteraceae has seen great effort recently to refine generic concepts including an effort to sort the true large genera from the false ones. This has resulted in much "splitting" that some botanists have dismissed as only part of a general trend toward more genera that has occurred throughout taxonomic history. However, closer examination shows that the primary force behind the recent efforts is the vastly increased knowledge that may sometimes reduce genera as well as "split" them. The fact that "splits" predominate is because many of the "garbage pit" genera, that often contain 1000 or more species, are receiving the first competent taxonomic study that they have ever had.

The generic level that has emerged from recent revision in the Asteraceae is generally close to that long established in the better known elements of the Family such as the Tribe Heliantheae. The latter tribe has long benefitted from more realistic generic concepts because of its wealth of obvious achene characters and its comparative cytological diversity tending to isolate groups. The only recent example of extensive splitting in the tribe has been in the Espeletinae (Cuatrecasas, 1976) where characteristics too large to preserve on herbarium sheets and lack of adequate field work had previously prevented realistic concepts.

In the Tribe Astereae, where generic concepts are in flux (Grau, 1977), some of the segregates from larger genera seem particularly flawed. The primarily dioecious neotropical genus Baccharus of ca. 400 species shows some variations in sexual expression and in paleaceous receptacles that have led to some unjustified generic segregates. In Aster, recent attempts to recognize Virgulus (Semple & Brouillet, 1980) solely on the basis of its $X = 5$ rather than $X = 9$ chromosome number, has been challenged by Jones and Young (1983). The work by Stucky and Jackson (1975) measuring DNA content and Gottlieb (1981) using isozymes supports Jones and Young in showing the chromosome variation does not involve ploidy levels but is rather a case of fragmentation-fusion that may be highly reversible.

Two Tribes that have particularly suffered from inadequate treatments in the past are the Liabeae and Eupatorieae. Both tribes are mostly Neotropical, an area like Australia that is poorly understood in Eurocentric treatments. Both tribes have also suffered from excessively artificial "core genus" concepts defined by what they are not rather than by what they are. In fact, the Liabeae were treated as four genera dispersed in four different tribes in the traditional treatments, none of the tribes being truly closely related. Both the Liabeae and Eupatorieae show that the past generic problems were only part of incompetent taxonomic treatments at all levels including species, genera, tribes, and subfamilies (Robinson, 1981, 1983; Robinson & King, 1977). In the Eupatorieae, among the genera surviving is Mikania, the largest in the tribe, with ca. 400 species. The genus has been changed only by the reduction of the artificial segregate Kanimia to synonymy. The genus is a model for taxonomists with its sharp distinctions based on obvious characters and its lack of phyletic complications with any other genus. Other Eupatorieae have not all been as well-defined, and the disposition of the 1000 species of Eupatorium is sometimes complex because the evolution of the tribe is complex. The ca. 100 new and revived genera in the tribe reflect the use of new evidence mostly from microcharacters as well as totally new discoveries in previously poorly explored areas showing taxa that are distinct even by traditional standards. The level of understanding previously seen in a few better known genera such as Stevia, Liatris and most of Brickellia has been extended to the previously artificial concepts that were Eupatorium, Ageratum, Piqueria, Alomia, Ophryosporus, and Eupatoriastrium.

Two other tribes worthy of note, the Vernonieae and Senecioneae, suffer from "core genus" concepts with a 1000 or more species. In the Vernonieae, Vernonia has grown to include many elements that exceed even what little definition the genus had, genera such as the paleaceous Lepidonia (Turner, 1981), and Distephanus (Gongrothamnus) (Jones, 1981) having basal appendages on the anthers and yellow flowers. Dismantling

the artificial concept of *Vernonia* has scarcely begun, but Jones (1977) has demonstrated basic differences between New and Old World members of the genus that will eventually have to be recognized at or above the generic level. The exact level that will be recognized is not certain since MacLeish (1985) has recently indicated the intent to treat as five genera a group Robinson (1980) treats as one.

In *Senecio* of the Senecioneae a large genus exceeding 1000 species is likely to survive the various efforts at subdivision by recent authors (Robinson & Brettell, 1973, 1974; Robinson & Cuatrecasas, 1978; Cuatrecasas, 1981; Jeffrey & Chen, 1984; and others).

To botanists less familiar with details of the Asteraceae, the large amount of change needed in the Family may seem surprising. They have no doubt been misled by the excessive claims of substance in the traditional systems or have heard the rationalisations of those actively suppressing change in the name of nomenclatural stability. Hopefully, the present efforts to apply new knowledge at the generic level in the Asteraceae and other families will achieve a real stability in nomenclature that all taxonomists can respect. Such a stability would be based on realities, and would not be a false stability of the type traditionalists have attempted to impose during the past 150 years.

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GENERIC CONCEPTS IN ASTERACEAE

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I shall consider some of the larger genera of Asteraceae to see how far they meet the criteria of being maximally informative (i.e. monophyletic), readily recognizable and nomenclaturally stable.

Artemisia L. (1753), type A. vulgaris L. (Europe), tribe Anthemideae, with 19 species on foundation now has about 400 (Airy Shaw 1966). The syndrome of characters associated with wind pollination has assured its coherence and apart from the necessary separation of the homogamous A. maritima-group as Seriphidium (Bess.) Pol. (Polyakov 1967), the above criteria are best met by retention of Artemisia as a large, natural genus.

Chrysanthemum L. (1753), type C. coronarium L. (Europe), tribe Anthemideae had 14 species on foundation, 200 in 1966 (Airy Shaw 1966), but only 2 in 1977 (Heywood & Humphries 1977). The growth of the genus was largely a result of the lumping by Bentham (1873), who included in it any non-paleaceous anthemid with several series of broad phyllaries and 5-10-ribbed achenes. Embryological (Harling 1951) and carpological (Heywood 1959, Tsvelev 1961) studies demonstrated its polyphyly and a rapid shedding of species resulted, many passing into Tanacetum L. which now has assumed some of the shortcomings of the Benthamic Chrysanthemum and may be an example of a paraphyletic residuum. The need for the florists' 'Chrysanthemum' to become Dendranthema has not unexpectedly caused resistance to change.

Aster L. (1753), type A. amellus L. (Europe), tribe Astereae, with 30 original species now has an estimated 500 (Airy Shaw 1966) and exemplifies the characteristic in Asteraceae of the existence within a tribe of a large, often name-giving core genus (e.g. Vernonia in

Vernonieae, Senecio in Senecioneae and, until recently, Eupatorium in Eupatorieae), surrounded by a fringe of numerous smaller satellite genera more or less widely recognized or sunk (see Grau 1977). Lack of clarity as to what are the group-defining characters or synapomorphies of such satellites has greatly limited their usefulness. Careful study of new features, such as those of the achenes (Grau 1971) and careful attention to the problems of homology are essential prerequisites of improvement. The cladistic study by Jones & Young (1983) is preliminary in scope but suggests that the recognition of a broadly circumscribed Aster is at present both avoidive of paraphyletic taxa and nomenclaturally convenient.

Baccharis L. (1753), type B. halimifolia L. (North America), tribe Astereae, is, like Artemisia, an example of a stable, well-characterized (shrubby and dioecious) large genus, the splitting of which (e.g. by the separation of the species with paleate receptacles into a distinct genus) would probably render the rest of the genus paraphyletic. About 500 species (Heras, 1976) are involved.

Osteospermum L. (1953), type O. spinosum L. (South Africa), tribe Calenduleae, was recircumscribed to include 70 species by Norlindh (1943) on the basis of female-fertility distribution in the capitulum. Baagøe (1977, 1978) has shown ray-floret epidermal microcharacters correlate with palynological, chemical and morphological differences suggesting a close relationship between species now referred to Castalis Cass., Dimorphotheca Moench and Osteospermum sect. Blaxium (Cass.) T. Norl. and that a reappraisal of generic limits is urgently required.

Centaurea L. (1953) type C. centaurium L. (Europe), tribe Cardueae, with 50 species on foundation now has about ten times as many. The work of Wagenitz (1955) and others has shown it to be characterized by a number of unique apomorphic pollen types, which together with other useful cytological and morphological variation has led to its splitting by some authors. The segregates have, however, not been generally accepted; though the splits are probably monophyletic, so also is Centaurea sens. lat. as accepted by Wagenitz; moreover, the type species is representative of a small, rather atypical and comparatively plesiomorphic section which means that when the genus is split, vast numbers of new, unfamiliar names enter the literature. Such nomenclatural discontinuity without gain in information favours the retention of a broad Centaurea.

Cousinia Cass. (1827), tribe Cardueae, with nearly 600 species is a genus practically confined to the Irano-Turanian region (type C. orientale (Adams) Koch from the Caucasus). It is closely related, however, to the mesic northern-boreal Arctium L. (1753), with about 10 species. Whether they are sister-groups or whether Arctium without Cousinia is paraphyletic is as yet unclear. Polyakov (1967) took the latter view and sunk Cousinia into Arctium*/without Cousinia would need to be unequivocally demonstrated. The pollen studies of Kupriyanova & Cherneva (1982) show only that some sections of Cousinia share a plesiomorphic type with Arctium, so the question is still open.

Helichrysum Mill. corr. Pers. (1754), tribe Inuleae, is a good example of a genus of Eurocentric foundation (type H. orientale (L.) Gaertn. from the Mediterranean) that has become artificially swollen to a gross extent. In the Helichrysum - Gnaphalium complex the true relationships of about 1000 species world-wide need to be resolved. It is unlikely that

African and Australian species now referred to Helichrysum will prove really congeneric; the same applies to Helipterum (itself an untenable name) (Georgiadou, unpubl.).

Senecio L. (1753), type S. vulgaris L. (Europe), tribe Senecioneae, is another example, and as core genus in the tribe, is less homogeneous and natural than Aster. Fortunately, chromosome numbers and anther-collar morphology provide some synapomorphies defining groups which can then be used as functional outgroups of one another and thus point the way to a better understanding of the tribe. The subtribes Senecioninae, Tephroseridinae and Tussilaginatae appear reasonably well-defined (Jeffrey & Chen 1984) but problems remain; e.g. Adenostylinae (n = 19, Adenostyles Cass. and Pojarkovia Askerova) probably require recognition, and the affinities of Packera Loeve & Loeve remain to be elucidated. Problems of paraphyly and of apomorphic tendencies in Senecio sensu stricto also remain, but the uselessness in biology of the traditionally-circumscribed Senecio is gradually being eliminated.

Vernonia Schreb. (1791) type V. noveboracensis (L.) Willd., tribe Vernoniaeae, from temperate North America, now has an estimated 1000 species. The Old World and New World species are biochemically, cytologically and, in many cases, palynologically distinct, these differences being made the basis of a division into two subgenera (Jones 1981). However, satellite African genera resemble the Old World Vernonia in these respects, so in effect there appear to be two major groups within the tribe - the Old World Vernonia and their satellites, and the New World Vernonia and their satellites, basically n = 9 or 10, and n = 17 respectively. Two as yet unresolved problems thus emerge - are these monophyletic sister-groups, or is part of one ancestral to the other; and should the major division be at subtribal level, rather than at the subgeneric?

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CLASSIFICATION AND GENERIC STATUS IN THE EPACRIDACEAE
- A PRELIMINARY ANALYSIS

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The Epacridaceae is a relatively large and diverse family and as with so many other families, the concept of genus has varied from time to time and from person to person. Traditionally the family has been split into 2 main tribes on the basis of ovary and fruit structure: the Epacrideae, with capsular fruits, and the Styphelieae, with drupes and pyrenes. The number of genera recognized has varied from c. 20-31, many of which are small, well-defined groups, or monotypic, while others are medium-sized and one, namely Leucopogon, is large. The total number of species is c. 450 or more.

In 1966-67 Watson et al reported on numerical analyses of the family (using some 20-25 characters, including leaf fibre pattern, nodal anatomy, stomatal distribution, inflorescence, pollen, flower and fruit characters) and suggested a reorganization at the tribal level and above, to define relationships more clearly (Figures 1 & 2). Our recent very preliminary cladistic analysis of the family leads us to agree with Watson on some groups but to disagree with him on the composition of others and/or on their status.

The analysis has used 41 characters, including habit, anatomical features (nodal anatomy, stomatal distribution and morphology, pith composition etc., following Watson (1967), Stevens (1971)), leaf structure, inflorescence type, flower structure (number and fusion of parts, aestivation, placentation etc.), pollen morphology and fruit type and

FIGURE 1. GENERIC CONCEPTS IN THE EPACRIDEAE S.LAT.

| BROWN (1810) | BENTHAM (1869) | MUELLER (1867-89) | WATSON (1967) |
|---------------------------------|-----------------|----------------------|-----------------|
| COSMELIA | * | * | ~) |
| PONCELETIA | COMBINED WITH | * | (COSMELIAEAE |
| SPRENGELIA | SPRENGELIA..... | COMBINED WITH | (Epacridoideae |
| ANDERSONIA | * | ANDERSONIA | .) |
| CYSTANTHE..... | COMBINED WITH | * | ~) |
| RICHEA | RICHEA | * | (|
| DRACOPHYLLUM Labill. | * | * | (Richeoideae |
| including SPHENOTOMA | * | * | .) |
| EPACRIS Cav. | * | * | ~) |
| ARCHERIA | * | COMBINED WITH | |
| Hook.f. (1844) | | EPACRIS | |
| LYSINEMA | * | * | |
| including WOOLLSIA..... | * | * | (EPACRIDEAE |
| | | F.Muell. (1872) | (Epacridoideae |
| PRIONOTES | * | * | |
| LEBETANTHUS..... | | COMBINED WITH | |
| Endl. (1841) | | PRIONOTES | |
| | | by Skottsberg (1916) | |
| RUPICOLA Maiden & Betche (1898) | | | |
| "BUDWANGIA" Telford ined. | | | .) |

FIGURE 2. GENERIC CONCEPTS IN THE STYPHELIEAE

| BROWN (1810) | BENTHAM (1869) | MUELLER (1867-89) | SLEUMER (1964) & VIRET (1975) | WATSON (1967) |
|----------------------|-------------------|-------------------|----------------------------------|-----------------|
| NEEDHAMIA (-IELLA) | * | * | | NEEDHAMIELLIEAE |
| OLIGARRHENA | * | * | | OLIGARRHENEAE |
| DECASPORA..... | COMBINED WITH | * | | ~) |
| TROCHOCARPA | TROCHOCARPA..... | COMBINED WITH | | |
| PENTACHONDRA | * | PENTACHONDRA | * | |
| | | DECATOCA | * | |
| | | Mueller (1889) | | |
| MONOTOCA | * | ~) | | |
| ACROTRICHE | * | | ~) | |
| STYPHELIA Sm. | COMBINED WITH | | | |
| SOLENSCIA | | COMBINED | | |
| DC. (1838) | | INTO | (sections of | |
| ASTROLOMA Cav..... | COMBINED WITH | A | (STYPHELIA | |
| STENANTHERA | STENANTHERA | SINGLE | | |
| MELICHRUS | * | GENUS | .) | (STYPHELIEAE |
| CYATHODES Labill. | * | STYPHELIA | ~) | (Epacridoideae |
| LEUCOPOGON | * | | | |
| LISSANTHE..... | PART COMBINED | | (subgenera of | |
| WITH BRACHYLOMA..... | | | (STYPHELIA | |
| Sonder (1844) | | | | |
| CYATHOPSIS | .) | | .) | |
| B&G (1864) | | | | |
| CONOSTEPHIUM..... | DISTINCT | | | |
| Bentham (1869) | BY 1889 | | | |
| COLEANTHERA | DISTINCT | | | |
| Stschegl. (1859) | BY 1889 | | | |
| | | CHORISTEMON | | |
| | | Williamson (1924) | .) | |

TABLE 1. EPACRIDACEAE- CHARACTER LIST

| | ADVANCED (1) | PRIMITIVE (0) |
|---------------------------|--------------------|--------------------------------|
| 1. HABIT | CLIMBER | SHRUB |
| 2. LEAF SCARS | ABSENT | PRESENT |
| 3. HAIR TYPE | UNICELLULAR | MULTICELLULAR |
| 4. LEAF INSERTION | SHEATHING | NON-SHEATHING |
| 5. LEAF VENATION | PARALLELODROMOUS | CAMPTODROMOUS ACTINODROMOUS |
| 6-9. LEAF T.S. TYPES | | |
| 6. STYPHELIA PATTERN | PRESENT | ABSENT |
| 7. EPACRID PATTERN | PRESENT | ABSENT |
| 8. COSMELIA PATTERN | PRESENT | ABSENT |
| 9. RICHEA PATTERN | PRESENT | ABSENT |
| 10. NODAL ANATOMY | MULTILACUNAR | UNILACUNAR |
| 11. PITH COMPOSITION | HOMOGENEOUS | HETEROGENEOUS |
| 12. STOMATAL MORPHOLOGY | ANOMOCYTIC | ABSENT |
| 13. | PARACYTIC | ABSENT |
| 14. | CYCLOCYTIC | ABSENT |
| 15. STOMATAL DISTRIBUTION | ABAXIAL + ADAXIAL | ABAXIAL ONLY |
| 16. FLOWER PART NUMBER | TETRAMEROUS | PENTAMEROUS |
| 17. FLOWERS PEDICELLATE | | |
| ABOVE UPPERMOST BRACTS | ABSENT | PRESENT |
| 18. CALYX TYPE | FLESHY | DRY |
| 19.) PETAL TYPE | FUSED | FREE |
| 20.) FUSION TYPE | SPLITTING AT BASE | FUSED |
| 21. AESTIVATION | VALVATE | IMBRICATE |
| 22.) ANTHOR NUMBER CF. | EQUAL OR LESS THAN | TWICE PETALS |
| 23.) PETAL NUMBER | LESS THAN | EQUAL |
| 24. ANTHOR COHERENCE | COHERING | FREE |
| 25. ANTHOR CELL NUMBER | 1-CELLED | 2-CELLED |
| 26.) FILAMENT INSERTION | INSERTED | FREE |
| 27.) IN COROLLA | INSERTED IN THROAT | INSERTED IN BASE |
| 28. ANTHOR DEHISCENCE | PORES | LONGITUD. SLITS |
| 29. STYLE LENGTH | SHORT | LONG |
| 30.) OVARY CELL NUMBER | GREATER THAN 5 | LESS OR = 5 |
| 31.) | LESS THAN 5 | 5 |
| 32. NUMBER OVULES /CELL | ONE | 2 - MANY |
| 33. PLACENTATION | APICAL | AXILE |
| 34. NECTARY | ABSENT | PRESENT |
| 35.) FRUIT TYPE | DRUPE OR PYRENE | CAPSULE |
| 36.) | PYRENE | DRUPE |
| 37. FRUIT MESOCARP | FLESHY | DRY |
| 38.) POLLEN APERTURE | PORATE OR INAPERT. | COLPORATE |
| 39.) | INAPERTURATE | PORATE |
| 40.) INFLORESCENCE TYPE | BLASTOTELIC | ANTHOTELIC |
| 41.) | AUXOTELIC | ANAXOTELIC |

structure (Table 1). Polarization of the character states was done where possible by outgroup comparison (Watrous & Wheeler 1981, Stevens 1980) with the Ericaceae (Stevens, 1971) and Clethraceae, and by functional outgroup analysis after an initial cladogram was constructed (Watrous & Wheeler op. cit., Maddison et al, 1984, Weston et al, 1984).

The taxa included in the analysis were considered to be monophyletic, and were either genera or groups of species within genera. The data matrix was analysed using Felsenstein's PHYLIP package as well as Wagner 7B and the cladogram presented is one of the most parsimonious formed and has a high level of consistency.

The preliminary analysis of the family indicates that the Epacridaceae is monophyletic if Wittsteinia is removed.

Wittsteinia F.Muell. is a monotypic genus found only in Victoria. Considered to be in the Ericaceae by Bentham (1869, tribe Vaccinieae) and Drude (tribe Arbutoideae), Wittsteinia was transferred to the family Epacridaceae by Burt (1948) to form part of the tribe Prionoteae. Watson

(1967) considered it as a separate tribe, Wittsteinieae, within his subfamily Epacridoideae of the Epacridaceae but Stevens (1971) returned it to the Ericaceae at subfamilial rank.

Our cladistic analyses indicate that Wittsteinia is quite distinct from Prionotes and Lebetanthus and is better placed within the Ericaceae. Most recently it has been considered as part of another family, the Alseuosmiaceae (Steenis, 1984), and given the number of apomorphies defining it in our diagram this suggestion certainly warrants further investigation.

I. The EPACRIDEAE s.lat.

Within the Epacrideae s. lat. there has been relatively little disagreement over generic limits, some 11-14 genera being recognized, with a total of c. 148 species. There are 4-5 monotypic genera (Cosmelia, Woollsia, Prionotes, Lebetanthus and "Budawangia") and low species numbers in all other genera except Andersonia (22), Epacris (c. 40), and Dracophyllum (c. 47).

The cladistic analysis shows two monophyletic groups within the traditional tribe, and several subgroups (Figure 3).

A. The RICHEA and COSMELIA groups

The two groups, traditionally in the tribe Epacrideae, were split up by Watson (1967): Richea, Sphenotoma and Dracophyllum formed his subfamily Richeoideae, while Cosmelia, Sprengelia and Andersonia formed his tribe Cosmelieae within subfamily Epacridoideae.

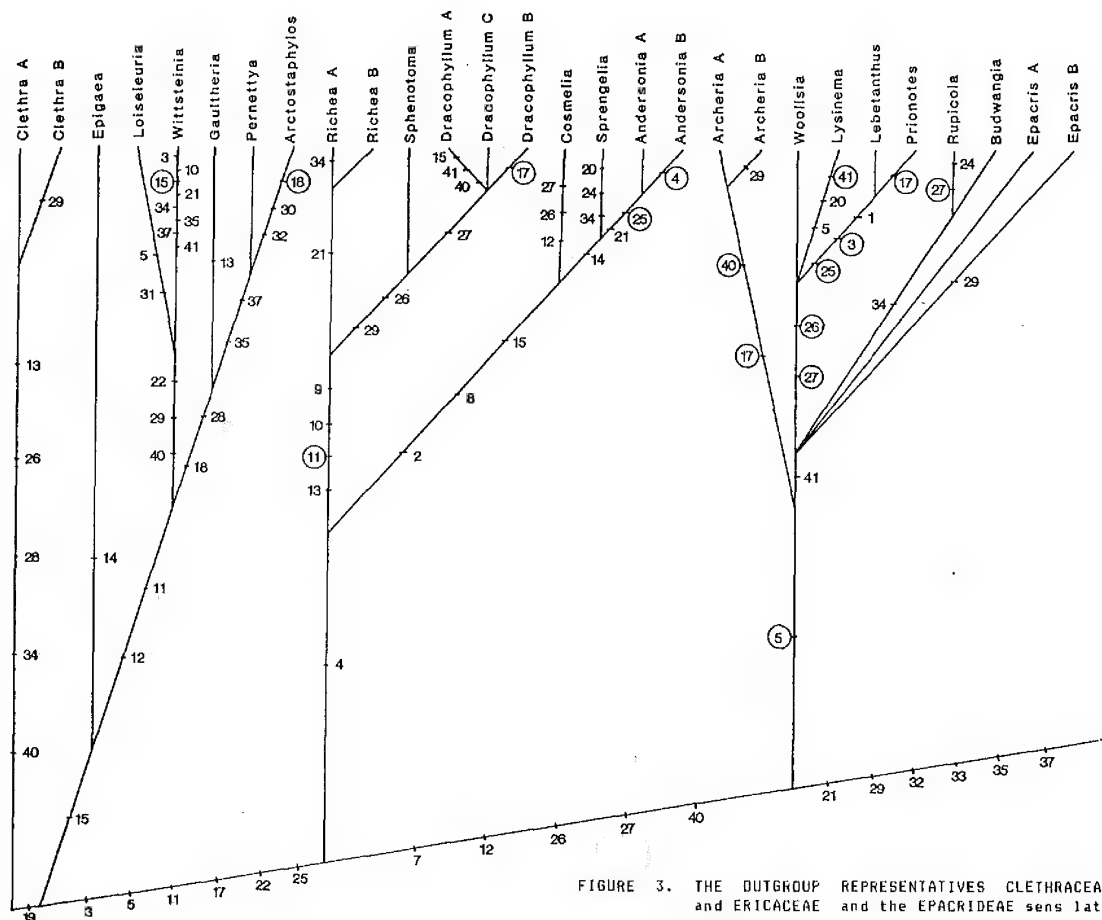
Our analyses suggest that these two groups are of equal rank and together could be considered to form a tribe, or perhaps subfamily.

There appear to be no generic problems here:

1. There seems little reason to separate Cystanthe (Richea A) from Richea (Richea B),
2. Dracophyllum and Sphenotoma can be readily separated on the basis of filament insertion and other floral characters not used in the analyses.
3. Subgenus A of Dracophyllum may be worthy of generic rank given the number of apomorphies shown; further work is needed on this group.
4. Cosmelia is distinct.
5. Sprengelia has a number of apomorphies, Andersonia some, so they should remain separate.
(Insert Fig. 3.)

B. The EPACRIS group

This monophyletic group forms Watson's tribe Epacrideae within his subfamily Epacridoideae. The group needs further study, particularly in light of the number of character reversals shown. This suggests problems with homologies, although an alternative interpretation is that this is



the most primitive group in the Epacridaceae. In a few cladograms this group did appear before the Richea-Cosmelia group but these cladograms were less parsimonious. At the generic level:

1. Archeria appears distinct and there is little point in combining it with Epacris, as Mueller did; if combined then all other taxa within this group would have to be included.
2. Lysinema and Woollsia are obviously closely related, but Lysinema has some apomorphies, indicating that it is distinct.
3. Lebetanthus and Prionotes form a closely related group but can be separated on ovary characters (no. ovules/loculus; placentation) not used in the analyses, as well as other vegetative and floral characters. Their distribution (South America and Tasmania respectively) suggests a long history of isolation.
4. Epacris groups A & B form a trichotomy with Rupicola and "Budawangia" and they are obviously closely related. Rupicola shows some apomorphies (anthers cohering, filaments inserted in the base of the corolla) and shares with "Budawangia" the absence of a nectary. Other characters not used in the present analysis also serve to distinguish each of these genera.

II. The STYPHELIEAE

A series of synapomorphies separate the earlier groups discussed from the remainder, which can be considered as the tribe Styphelieae, as traditionally grouped (Figure 4). It is mostly within this monophyletic group that generic concepts have varied. Robert Brown in 1810 listed 14 genera, and Bentham (1869) recognized 15 Australian genera and if the New Caledonian Cyathopsis is included, then 16 genera formed the group. Today, with more recent additions, 18 genera can be discerned, with a total of 270-320 species.

Mueller (1867-1889) accepted only some of these genera: Needhamiella, Oligarrhena, Decaspora (surprising since Bentham had sunk it into Trochocarpa), Cyathopsis; he combined Trochocarpa and Pentachondra and all others he considered as Styphelia. Later, in his Census (1889) he also accepted Conostephium and Coleanthera as distinct.

While some of the genera are monotypic (Needhamiella, Oligarrhena, Cyathopsis, Decatoca and Choristemon) most have only low species numbers (between 3-18); the exception is Leucopogon - it has always been large in comparison, (with 118 species being described for Australia by Bentham) c. 149 species, with c. 125 in Australia, 4 in N.Z., 13 in New Caledonia and 7 in Malesia (Sleumer 1964). Recent work on the Australian component suggests that there are some 200 species or more in the genus.

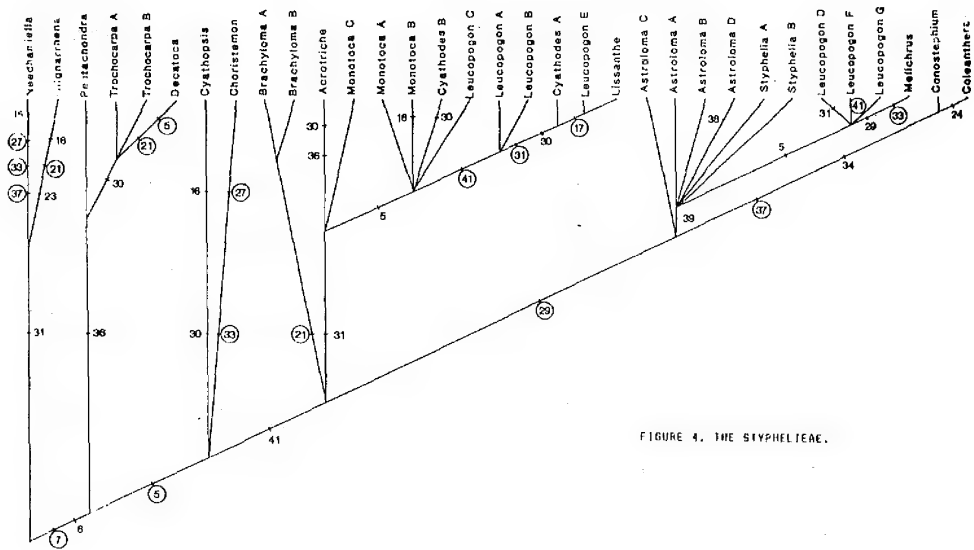


FIGURE 4. THE STYPHELTEAE.

If the broader generic concept of Mueller is accepted then Styphelia would comprise some 240 species and with recent additions, nearly 300 species.

The preliminary cladistic analysis can be discussed in this historical context. A number of sub-groups can be distinguished:

C.1. Needhamiella and Oligarrhena

Watson (1967) considered that these two monotypic Western Australian genera were each so distinct that they warranted tribal status,

equivalent to the Styphelieae, Epacrideae etc. within his sub-family Epacridoideae, and Jackes (1968), studying the organography and vascular anatomy of the flower agreed.

Our analyses suggest that the genera are distinct but do not warrant tribal status; they should be considered as part of the Styphelieae. In the most parsimonious cladogram these two genera appear as a group, on the basis of low ovary cell number (less than 5), but the value of this character requires further assessment. In other cladograms they appear as distinct entities and we would consider this to be more acceptable.

C. 2. Pentachondra, Trochocarpa and Decatoca

These taxa form a distinct subgroup. Historically, Mueller united Pentachondra with Trochocarpa but Bentham considered they differed in habit and inflorescence characters. Recent additions to Trochocarpa (Sleumer, 1964) bring the genera closer together.

Trochocarpa and Decatoca differ from Pentachondra mainly in ovary cell number, but other characters not used in the present analyses may help to separate them also, e.g. chromosome counts suggest differences with Trochocarpa (laurina) $n=10$, Pentachondra $n=13$ and $n=14$. While Decatoca appears to be distinct from Trochocarpa, some species of the latter are distally imbricate in bud; the group as a whole warrants further study.

The remaining subgroups, if taken together, reflect Mueller's initial concept of Styphelia. He later excluded Conostephium and Coleanthera (the two genera shown on the far RHS of the diagram).

C.3. Cyathopsis and Choristemon

Although grouped together, these two monotypic genera have a number of apomorphies and are generically distinct.

C.4. Brachyloma, Acrotriche, Monotoca, Cyathodes, Leucopogon A, B, C & E, and Lissanthe,

C.5. Astroloma, Styphelia, Leucopogon D, F & G, and Melichrus, and

C.6. Conostephium and Coleanthera.

The remaining part of the cladogram suggests some interesting groupings that cut right across the traditional genera of Brown and Bentham. In particular, it indicates that:

- a) the large genus Leucopogon is polyphyletic and should be split into at least two genera and possibly more,
- b) Astroloma and Styphelia form a polychotomy and could be combined to form a single genus,
- c) the present delimitation of both Monotoca and Cyathodes requires reassessment in relation to certain species groups of Leucopogon and to Lissanthe,
- d) Brachyloma, Acrotriche and Melichrus can remain as distinct genera, and
- e) Conostephium and Coleanthera form a well-defined clade. Their relationship to the Astroloma-Styphelia group can be seen in certain floral characters, and in most cladograms they appeared with that group.

Each has distinguishing features, however, and they can remain as distinct genera.

These last subgroups require further resolution that will only come with detailed analysis of characters to check homologies, and with the use of further characters. Traditionally the genera are defined on the basis of inflorescence structure, number and type of bracts subtending each flower, corolla tube shape, type and distribution of hairs on the corolla, corolla lobe aestivation, style length, filament type and position, anthers free or cohering, attachment point of the filament to the anther, and pulpiness and coherence of the fruit. In the present analyses we have used only a few of these characters (those italicized).

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GENERIC STATUS IN THE CHENOPODIACEAE

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Abstract

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The currently accepted classifications within the tribes Chenopodieae and Camphorosmeae of the Chenopodiaceae appear to be unnatural, particularly with reference to Australian genera. Some anomalies are noted and suggestions made for an improved taxonomy.

GENERIC STATUS IN THE CHENOPODIACEAE

The infrafamilial classification of the Chenopodiaceae has been a contentious issue and recently a number of attempts have been made to resolve the current unsatisfactory situation (Williams and Ford-Lloyd 1974, Blackwell 1977, Scott 1977a,b). Within Australia, now that the taxonomic position of the family Dysphaniaceae has been established (Eckardt, 1969) and some agreement reached on the genera in the tribe Salicornieae (Scott 1977, Wilson 1980), the problems at as generic and suprageneric level reside principally in the tribes Chenopodieae and Camphorosmeae and it is with these that this paper is concerned.

TRIBE CHENOPODIEAE

Recent proposals for the classification of the Chenopodieae (Scott 1978a, Wilson 1983) have not been satisfactory. Scott (1978a) recognised two subtribes, the Rhagodiinae and the Chenopodiinae but in doing so separated at the subtribal level species that appear to be closely related, while the very broad circumscription of Chenopodium of Scott (1978c) and Wilson (1983) places together species that have little in common. The situation obviously requires attention.

The genera currently recognised as being indigenous to Australia (Wilson 1984) are Atriplex, Chenopodium, Dysphania, Einadia, Rhagodia, and Scleroblitum. Both Atriplex and Chenopodium are world-wide in their distribution while the others are endemic to Australia and New Zealand.

With Atriplex sensu lato there is disagreement over the number of genera into which the Australian species should be segregated. Ulbrich (1934) recognised six genera (one of which has since been shown to have been based on a specimen of Portulacaceae). Allen (1937-1938) also recognised six genera, however, of those recognised by Ulbrich only two (Atriplex and Theleophyton) were retained, while two (Neopreissia and Haloxanthium) he sunk under Atriplex and one (Rumic astrum) he did not consider since he had seen no material. Allen described four new genera of which one was based on galled material of two species, specimens of which he had otherwise placed in Atriplex. Recent Australian floristic works have accepted only one or two genera in the Atriplex group while overseas authors, in dealing with introduced Australian species, generally recognise three or four genera. However, all treatments agree on the close relationship of those genera to each other.

The genus Chenopodium presents problems as to number of genera that should be recognised and problems as to whether Chenopodium sensu lato represents a monophyletic group. The species indigenous to Australia are currently (Wilson 1984) placed in five sections while a sixth section (Sect. Ambrina) is represented by introduced species. Two of the six sections contain taxa with glandular hairs while the other four contain taxa with a mealy indumentum formed from bladder-hairs. A segregation of sections based on hair type is supported by other less assessable characters found in the leaves, flowers and fruit, and appears to represent a fundamental divergence of phylogenetic significance (Carolin 1983, Weber 1985).

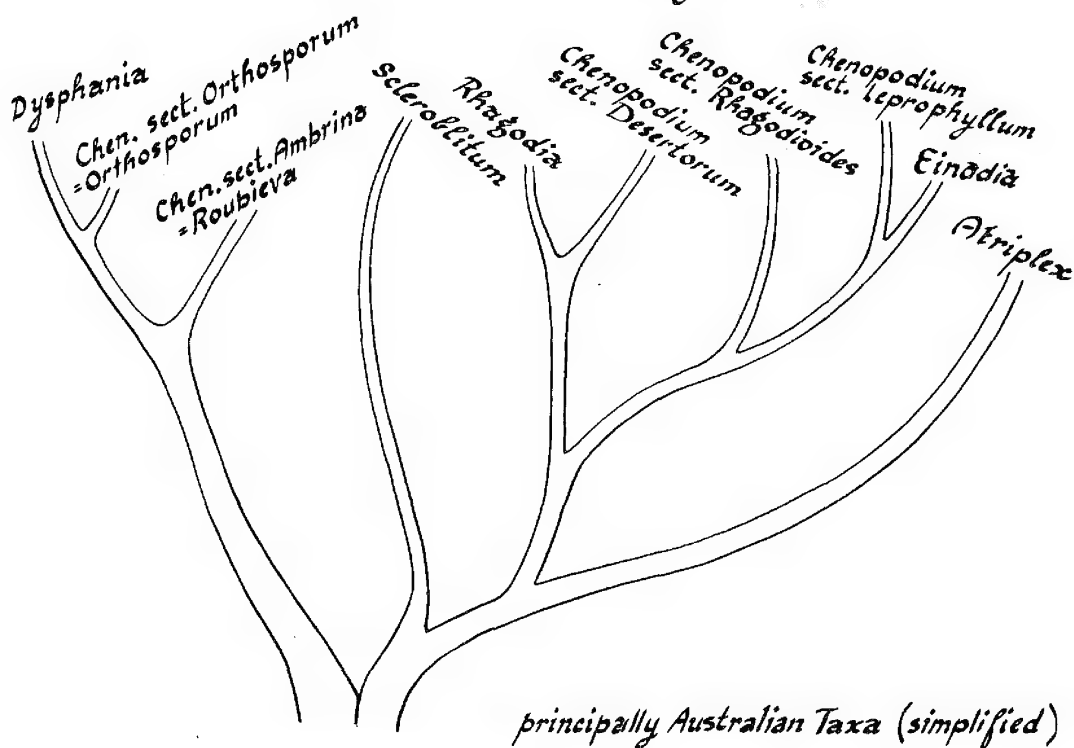
In Australia the 'glandular' taxa are found in sect. Ambrina (introduced) and sect. Orthosporum (endemic). The latter section is closely related to the genus Dysphania R.Br. (1810) and there is a graded series of species in which the flowers have 2 up to 5 tepals that links sect. Orthosporum to Dysphania. The species with 4 tepals which at present (Wilson 1984) are mainly placed in Dysphania could with equal justification be placed in sect. Orthosporum. If considered congeneric then Dysphania R.Br. (1810) is the correct name; if generically distinct then the 5-tepalous (? and 4-tepalous) species belong in Orthosporum (R.Br.) T.F.L. Nees (Dec. 1834). In early 1986 (Wilson 1986) I expressed the view that Chenopodium sect. Ambrina, to which belong the introduced South American species C. ambrosioides and C. multifidum, should be recognised as a distinct genus Roubieva Moq. (May 1834). Since then I have seen a paper by Weber (1985) who came to a similar conclusion but who adopted the name Teloxys Moq. (May 1834) into which he placed Roubieva; the two taxa had been previously separated at a generic or sectional level largely on the basis of the presence of spinescent branches in the inflorescence of Teloxys. Since the two generic names were published simultaneously Weber's choice should stand. Weber also suggested that the Australian species at present in sect. Orthosporum should be placed in Teloxys, however, I consider the two groups to be generically distinct and that the American species should be placed in Teloxys and the Australian in Dysphania (or Dysphania and Orthosporum). If Teloxys, Orthosporum, and Dysphania are amalgamated then the oldest name Dysphania R.Br. (1810) should be adopted.

The Australian species of Chenopodium that have a mealy indumentum are currently placed (Wilson 1984) in sect. Desertorum, sect. Leprophyllum, sect. Auricomma, and sect. Rhagodioides. The species placed in Chenopodium sect. Desertorum have much in common with the species placed in the genus Rhagodia, in particular perennial or shrubby habit, mealy indumentum, leaf shape, pentandrous flowers, horizontal seeds, and frequent

Chenopodiaceae tribe Chenopodieae

Glandular Taxa

Mealy Taxa



possession of a succulent pericarp. In fact, species correctly belonging to one group are often misidentified as species of the other. With the genus *Einadia* Raf. (1838) other problems arise. Some *Einadia* species have a fleshy pericarp and these have generally been recognised as belonging to *Rhagodia*, while others have a dry pericarp and these have been placed in *Chenopodium* (section *Polygonoidea*). The species belonging to the two groups are so similar, other than in pericarp character, as to be frequently difficult to separate, they have in common a perennial habit, mealy indumentum, reduced stamen number and horizontal seeds. While it would appear to be a correct decision to recognise them as constituting one taxon of generic or sectional rank it is also apparent that they are more closely related to both *Chenopodium* sect. *Leprophyllum* and to *Rhagodia* than they are to the glandular members of the genus *Chenopodium*. A nomenclature that reflects a more natural classification of the Australian 'mealy' members of the *Chenopodium* complex is required but it is unclear as to whether this is better achieved by raising the various sections to generic rank or whether the circumscription of *Chenopodium* should be expanded to encompass genera such as *Einadia* and *Rhagodia*. This matter is difficult to resolve in isolation since a number of extra-Australian sections and genera are involved.

TRIBE CAMPHOROSMEAE

The native species of the tribe Camphorosmeae are currently (Wilson 1984) placed in 14 genera all of which are endemic to Australia. The

delineation of these genera is based largely on the morphology of the fruiting perianth. This organ varies considerably in shape, texture, and in the nature of its appendages that may take the form of wings, spines, or other outgrowths. The present method of classifying the Camphorosmeae, based on these readily observable fruiting structures, provides a relatively simple means of determining genera. However, a dependence on these features in constructing a classification, as that by Scott (1978b), can result in closely related species being generically separated and even placed in different tribes or subtribes.

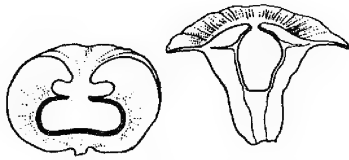
When considering the merits of these attempts to classify the Camphorosmeae it was at an early stage apparent (Wilson 1975) that the position of a perianth appendage was of more significance than its form; this conclusion led to a proposal that the Australian species of Bassia should be recognised as being generically distinct from the Eurasian and that the Eurasian species of Kochia and Bassia should be considered as being congeneric. Subsequently it became very obvious that among Australian species the presence of spines or wings, or the absence of both, was not necessarily of generic significance. Therefore (Wilson 1984) the genus Babbagia F. Muell. (1859), whose species have fruits with vertical wings intertepaline in position, was placed under the older name Osteocarpum F. Muell. (1858) whose type species has hard unappendaged fruits and for this reason was commonly included in Threlkeldia (T. salsuginosa). At the time it was apparent that some species of Sclerolaena with spiny perianths were also closely related to Osteocarpum; these species had a similar vegetative morphology and similar perianth structure except that spines were formed in the positions occupied by wings in Osteocarpum species. When writing up the Chenopodiaceae for the Flora of Australia no action was taken with these species since it was obvious that a number of other generic anomalies existed which to correct would together cause considerable changes in the classification of the Australian Camphorosmeae and the provision of a key to the groups that would eventuate presented a considerable problem. It has been possible to aggregate many of the Camphorosmeae species into apparently natural groups, however, it has not yet been possible to classify all taxa nor to satisfactorily assign a taxonomic rank to the groups. For this reason I consider it to be best to refrain from making generic transfers until the Australian Camphorosmeae are fully surveyed. The following species aggregates represent some preliminary thoughts on the establishment of a more natural classification; in each group species from two or more genera, as currently recognised, are involved.

1. Enchylaena group.

Enchylaena tomentosa (the type of Enchylaena) has a succulent perianth with an infolded succulent wing; in vegetative and flower morphology it is similar to Maireana georgei and M. turbinata; it hybridizes with both species.

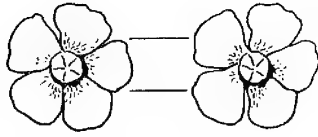
2. Threlkeldia diffusa group

Threlkeldia diffusa (the type of Threlkeldia) has a succulent outer fruiting perianth and an inner woody layer; the perianth, when dry, has a number of apical knobs. In vegetative and flower morphology this species is similar to Sclerolaena recurvuspis and S. fusiformis; in these species the outer perianth soon hardens and at the apex are borne spines in the positions occupied by knobs in T. diffusa.

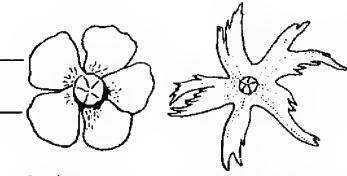


Enchylaena L.S. *Maireana* L.S.

Enchylaena



Maireana *amoena*



Maireana *amoena*



Maireana *luehmannii*

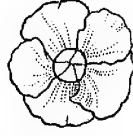


Bassia *sect.* *Spinosissima*
flowers in pairs

Sclerolaena *fimbriolata*



Roycea



Maireana *oppositifolia*

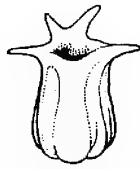


leaf

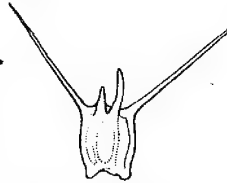
Roycea



Threlkeldia *diffusa*



Sclerolaena *recurvicaulis*



Sclerolaena *fusiformis*

Threlkeldia



Threlkeldia *salsuginosa*



Babbagia *acroptera*



Sclerolaena *urceolata*



Sclerolaena *anisacanthoides*

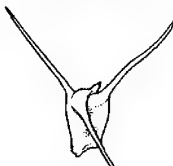
Ostocarpum



Threlkeldia *inchoata*



Sclerolaena *glabra*



Sclerolaena *cuneata*

Anisacantha

CHENOPODIACEAE TRIBE CAMPHOROSMEAE
(SOME AUSTRALIAN GROUPS)

3. *Threlkeldia inchoata* group.

Threlkeldia inchoata in leaf, flower, and fruit morphology resembles *Sclerolaena cimeata*, *S. divaricata* (the type of *Anisacantha*) and similar species of *Sclerolaena*. *Threlkeldia inchoata* appears to be a spineless member of a group in which the other members have spiny perianths.

4. Roycea group.

This group contains the three species of Roycea and Maireana oppositifolia. All species have similar leaves (trigonous with clawed base), indumentum, and flowers. In Roycea spp. the perianth scarcely changes in fruit while in M. oppositifolia it enlarges and develops 5 spreading wings.

5. Maireana amoena group.

This group consists of a number of species with paired axillary flowers, free epitepalous wings or spines, and leaves with a similar shape and indumentum. Some members of this group are Maireana amoena, M. luehmannii, M. scleroptera, and Sclerolaena fimbriolata (syn. S. symoniana). Hybridization between Maireana amoena and Dissocarpus paradoxus is well-documented and not uncommon in the Eremaean region of Western Australia. The hybrids appear to be sterile and have deformed fruits that have somewhat different morphologies in different areas, presumably due to the variability of M. amoena. It is probable that the type of Sclerolaena georgei is such a hybrid. Maireana amoena and D. paradoxus have much in common, i.e. more than one flower in leaf-axil, perianth appendages arising beneath perianth lobes, and horizontal seeds. It is possible that the two groups are more closely related than their superficial appearances would suggest.

6. Neobassia group.

The genus Neobassia currently contains two species, N. astrocarpa and N. proceriflora. With these species also belongs Sclerolaena clelandii, a plant similar in indumentum, fruiting perianth (with vertical seed), and position of perianth spines (epitepalous). In S. clelandii the spines arise below the perianth lobes but then fuse to form an abaxial group of 2-3 and an adaxial group of 2. This fusion of the spines, combined with the dorsiventral compression of the perianth, obscures their epitepalous origin.

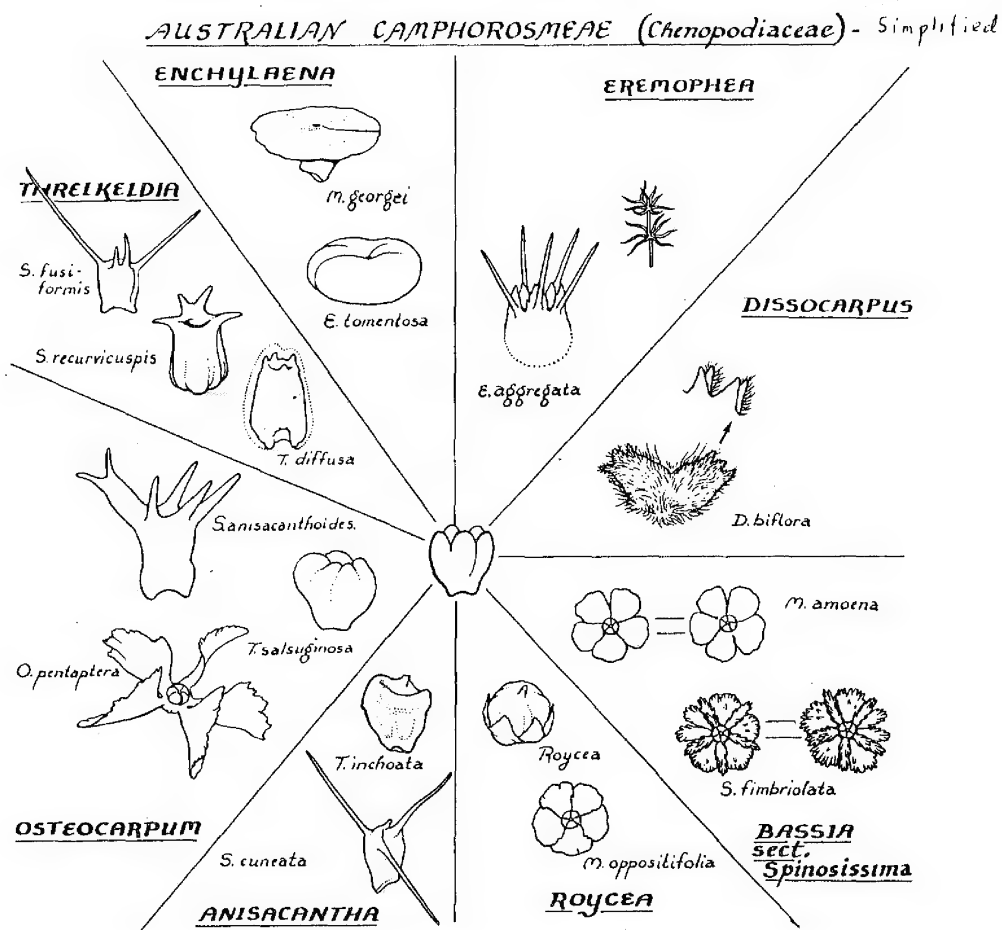
7. Sclerochlamys group.

Several species of Australian Camphorosmeae have a short barrel-shaped fruiting perianth with a broad horizontal attachment and flat horizontal apex; the seeds in each are horizontal. Around the apical margin of the perianth arise appendages whose varied nature has caused the species to be assigned to one or other of three genera, viz. Sclerochlamys (S. brachyptera), Stelligera (S. endecaspinis), and Sclerolaena (e.g. S. microcarpa). Three species have similar leaves and indumentum and should be recognised as congeneric. Some species of Maireana may also belong here.

8. Osteocarpum group.

The recognition of Osteocarpum (type O. salsuginosum) as being generically distinct from Threlkeldia and the transfer to it of the Babbagia species (Wilson 1984) unites two closely related taxa. To this group also belong some species of Sclerolaena, e.g. S. anisacanthoides and S. urceolata, that differ from the species at present in Osteocarpum in possessing spines and not wings.

This outline of intergeneric problems in some Australian members of the tribe deals with only a few of the species involved. For most, precise affinities have still to be assessed, when this is done a ranking of the



resultant groups can be presented and names applied at the genus level. However, even at this stage in the investigation it is obvious that unless generic groups are very broadly established their delineation will be difficult, and, if broadly established, their acceptance is likely to be minimal.

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CASSIA ... one genus or three?

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Adelaide

The genus *Cassia* Linnaeus sensu lato is widespread, occurring in South, Central and North America, southern, central and north Africa, Australia, the Pacific Islands, and the southern extremities of the Asian continent. As presently recognised it contains some 600 species. These exhibit a very wide array of morphological features. Australian cassias vary from rainforest trees with pendant 50-60-flowered racemes, to herbaceous plants a few centimeters high, with 1-2-flowered peduncles, in semidesert areas of Western Australia.

Recent proposals to recognise three genera (*Cassia*, *Senna* and *Chamaecrista*) within *Cassia* s.l. have met with a cool reception. However, I believe that this response has been due to lack of information in the following areas:

1. The historical background to the use of three names, or one name, is not known.
2. The morphological characters which can be used to separate the three genera have not been clearly stated.

In this report, I will attempt to provide information in both these areas.

Historical Review

The three generic names *Cassia*, *Senna* and *Chamaecrista* have a long history in the herbal literature. For example Mathioli (1570) and Dodonaeus (1583) (both cited by De Wit 1955), and Miller (1754) state that the name *cassia* was applied to plants with long woody and indehiscent pods whose pith was used as a purgative (ie. *Cassia fistula*). On the other hand, *senna* was used to name the plant whose short dehiscent pods were used as a purgative, and whose leaves were used to prepare skin treatments (ie. *Senna alexandrina*).

Breyne (1678) described several new species, in *Cassia*, and in *Chamaecassia* (this genus included plants closely related to *Senna alexandrina*). He also coined the name *Chamaecrista*, and placed in this genus herbaceous species related to *Cassia mimosoides*.

characters used by Irwin & Barneby to define 3 genera

| Character | <u>Cassia</u> | <u>Senna</u> | <u>Chamaecrista</u> |
|---------------|---|--|---|
| | Bilaterally symmetrical | Bilaterally symmetrical | Never bilaterally symmetrical |
| | Filaments of lower whorl elongate and sigmoidal | Filaments of upper whorl elongate and arcuate | Filaments never elongate |
| Androecium | All anthers dorsifixed | All anthers basifixed | All anthers basifixed |
| | Some anthers with apical and basal pores | All anthers with apical pores <u>only</u> | All anthers with apical pores <u>only</u> |
| | Anthers <u>never</u> beaked | Sometimes some anthers beaked | Anthers <u>never</u> beaked |
| Pods | Woody, indehiscent | Flattened and dehiscent; or terete, pithy and dehiscent; or woody and indehiscent (but then leaf glands present) | Flat, elastically dehiscent |
| Leaf Glands | Absent | Present or absent | Present or absent |
| Inflorescence | Terminal | Axillary | Axillary |
| Bracteoles | Present | Absent | Present |
| Root Nodules | Absent | Absent | Sometimes present |

Tournefort (1700) also recognised two groups, using Senna for the herbal plant long known by that name, and Cassia for C. fistula. However, he did include some plants, now known to be related to Senna, in his listing of cassias, probably as a result of misidentification.

Linnaeus however, treated all three names as synonyms, retaining Cassia and attributing its use to Tournefort. In *Genera Plantarum* edn 4 (1754) he included in the generic protologue, a clear and detailed description of a particular form of the androecium (unfortunately of a senna-type species) even though he had already published descriptions of several species which did not have this androecial structure. This generic description is a source of problems in choosing a lectotype species for the name Cassia.

With the expansion of botanical exploration in the eighteenth and nineteenth centuries, the number of species placed within Cassia (even though they did not have the androecial structure described by Linnaeus) grew rapidly. Bentham's revision (1871) listed more than 300 species. As the numbers grew, attempts were made to delimit smaller groups within Cassia, but were only partly successful. It was easy to recognise the Chamaecrista group, because their pods always dehisce explosively, and the valves subsequently show spiral coiling. However the separation of Cassia and Senna is not so easily accomplished.

Early attempts to separate Cassia and Senna relied heavily on the single character difference 'pods woody and indehiscent/pods dehiscent'. However, this character does not always correlate well with other traits such as plant habit, inflorescence structure, anther arrangement, and the occurrence of leaf glands. Hence most workers were not prepared to recognise these groups as genera, and they were treated at infrageneric levels by Lamarck (1783), Colladon (1816) Vogel (1837)

Bentham (1871) Symon (1966) and others. A few attempts were made to solve the problem by recognising many groups within Cassia (eg. Britton and Rose (1930) recognised 29 genera but this treatment failed when species from areas outside North America were examined).

Recently Irwin and Barneby (1982) proposed using the structure of the androecium as the chief diagnostic character to separate Cassia and Senna. This structure correlates well with other morphological characters and also enables the diagnosis of Chamaecrista (Table). The correlations between the androecial characters are maintained in India (Roxburgh 1832), in East Africa (Brenan 1967), in the Americas (Irwin and Barneby 1982), and in Australia (Randell unpubl.). The groups defined by these characters are so clear, the character correlations are so strong, and the geographical applicability of the characters is so wide, that it is appropriate to rank the segregates as separate genera.

However, as noted earlier, Linnaeus' protologue for the name Cassia included descriptions of only one of the androecial variants known to him. This has raised a problem in lectotypification, which is now being addressed.

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GENERIC STATUS OF ACACIA SENSU LATO

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The type species of the name Acacia, A. nilotica, was described by Linnaeus as a Mimosa. Acacia has a pre-Linnean history, but the name was validated by Philip Miller early in 1754 shortly after the publication of Species Plantarum. He was not generally followed, and it was not until Willdenow's adoption of Acacia for the fourth edition of Linnaeus's

Species Plantarum in 1806 that it gained respectability. In 1824 de Candolle also used it in his Prodrum and its permanent standing was ensured. De Candolle's concept of the genus was wide and unacceptable to later workers. He included species of Albizia, Pithecellobium and other mimosoid genera.

In a series of papers from 1842 to 1875, Bentham developed a classification of the genus which remained substantially unchanged for almost a century. Wight and Arnott had already described the genus Vachellia to accommodate A. farnesiana. In the first edition of Die Pflanzenfamilien, Taubert raised Bentham's series to sections but otherwise adopted his classification in toto. Bentham had "in vain sought for any better mode of distributing the species than in series, founded chiefly on foliage and inflorescence." Spegazzini described Manganaroa to accommodate some Argentine species. Britton and Rose took the most radical view of Acacia, recognizing eight new genera and taking up some genera of Rafinesque. Chevalier placed A. albida in the monotypic genus Faidherbia on what appeared to be mostly ecological grounds. None of these later workers considered the genus as a whole. All dealt with the species in only a relatively small geographical area. Mueller and Maiden described many species and both must have had a sound knowledge of the genus. Neither however, modified Bentham's classification to any significant extent.

In the late 1960's and 1970's the classification was seriously questioned by workers in France. In a survey of the pollen of the Mimosaceae Guinet found evidence for the removal of Faidherbia from the Acacieae to the Ingeae and suggested the splitting of Acacia into three genera. Vassal, using Guinet's pollen data and other morphological characters recognized three subgenera of Acacia which correspond to groups of Bentham's series. Vassal's subgeneric classification has been widely accepted.

The papers of Guinet and Vassal and some work on the flavonoid compounds of Acacia by Tindale and Roux led me to consideration of the classification of the genus. Prior to this I had been concerned mainly in taxonomic problems at the species level. My studies have been limited to the study of herbarium specimens and to field studies (chiefly in Queensland), but in reviewing the classification of Acacia I have tried to take into account anything published on the biology of its species. I believe that Guinet was correct in suggesting that Acacia be split into three genera and consider that the subgenera recognized by Vassal be given generic status. Published information on Faidherbia is scanty but it seems also to warrant recognition as a genus. The classification and its relationship to Bentham's final one and Vassal's are given below.

Evidence for the recognition of Senegalia Rafinesque and Racosperma Martius as genera distinct from Acacia is being published elsewhere. Morphology, palynology, chemotaxonomy, susceptibility to rusts have all been considered. The characters of the pollen, the free amino acid composition of the seeds and the structure of the inflorescences are considered important.

There seems to be some agreement among plant taxonomists about what a species is though some would hesitate to define one. As this conference has shown, the circumscription of genera is a matter of considerable debate. The recognition of narrowly circumscribed genera in large and

| Bentham | Vassal | Proposed |
|----------------------|--|-------------------------|
| series Gummiferae | subgenus <i>Acacia</i> | genus <i>Acacia</i> |
| series Vulgares | subgenus <i>Aculeiferum</i> | genus <i>Senegalia</i> |
| series Filicinae | | |
| series Phyllodineae | subgenus <i>Heterophyllum</i> | genus <i>Racosperma</i> |
| series Botrycephalae | (=subg. <i>Phyllodineae</i> (DC.) Seringe) | |
| series Pulchellae | | |

economically important families is a modern tendency. Casuarinaceae, Fabaceae (sensu stricto), Myrtaceae and Proteaceae are examples. Size alone is not a reason for splitting genera: there are some genuinely large ones. *Astragalus* (2000 species) and *Crotalaria* (600) come to mind. Often because of historical rather than biological factors distinctions between genera in families such as Brassicaceae, Orchidaceae and Poaceae are much finer than they are in other families. There appears to be no serious objection to this. There does appear to be a need for distinctions among genera of the same family, or at least some part of a family, to be comparable.

In an attempt to decide whether *Acacia* sensu lato was of a size consistent with other genera of the Leguminosae Williams's "Index of Diversity" (α) was applied to some tribes of the family. Comparison of the *Acacieae* with the *Ingeae* was considered likely to be of most value. The two tribes are only doubtfully distinct and generic limits within the *Ingeae* have been under examination in recent years. The index is probably of limited value but it was used in attempt to bring some objectivity to determining whether a split of *Acacia* was justified. It does suggest that, if three genera are recognized in the *Acacieae* (*Acacia*, *Racosperma* and *Senegalia*) and the tribe were united with the *Ingeae* then a value (4) in keeping with that of other tribes of low diversity (for example, *Cassieae*, *Cercideae*, *Calegeae*) would result.

The major consideration in dividing large, well-known, widely cultivated and economically important genera such as *Acacia*, *Casuarina* and *Eucalyptus* is not the taxonomic justification for the division but rather the social effect of such a change. *Racosperma* is a genus of more than 850 species, all but about nine native of Australia (The status of some Hawaiian taxa is uncertain). The other genera, *Senegalia* with two species in Cape York Peninsula and *Acacia* with about eight species in Northern Australia, are not well represented in the Australian region. They are

important components of the floras of southern Asia, Africa and tropical and subtropical parts of the Americas. Species of Racosperma are widely cultivated as ornamentals, for tan bark and, in recent years, as a potentially important forestry crop for the tropics. Some species are naturalised in New Zealand, South Africa and south-western Europe.

Adoption of unfamiliar generic names will cause disruption of communication among workers, particularly horticulturalists and foresters who may not appreciate the reason for change. I have spoken to several groups in Australia on the changes. Most people appear unconcerned about the change, involving as it does in most cases the substitution of one generic name for another. The formal transfer of names from Acacia to Racosperma and Senegalia as required by the International Code of Botanical Nomenclature will be a large and quite unproductive task. My attention has already been drawn to the high cost of curating herbaria with a large number of new names. It has been suggested that Vassal's subgeneric classification is sufficient to show the relationships of the major groups of Acacia with no alteration of the nomenclature. If any of these social, commercial or financial considerations are sufficiently strong then there will be no change. However I believe the interest of practising scientists can best be served by recognizing three genera, not three subgenera.

Biologists working in fields related to, but distinct from, botany often have plants identified. Often these plants are hosts for other organisms. Quite rightly they believe that species bearing the same generic name are more closely related to each other than species bearing different generic names. They are often not in a position to search the literature for the relationships of individual species. A list of five species, Acacia albizioides, A. confusa, A. farnesiana, A. nilotica, and A. penninervis, is likely to be regarded quite differently than a list of the same species arranged in the segregate genera: Acacia farnesiana, A. nilotica, Racosperma confusum, R. penninerve and Senegalia albizioides.

Speculation about phylogeny and biogeography are hampered by the acceptance of a large heterogeneous genus Acacia. A recent work on the vegetation of Australia suggests that Acacia ser. Gummiferae (that is Acacia sensu stricto) were directly derived from this stock. The widespread belief that species of Acacia sensu lato are primitive and more closely related to each other than they are to phyllodineous species suggests that Acacia section Pulchellae and Acacia section Botrycephalae were derived from either Acacia subg. Acacia or Acacia subg. Aculeiferum and in turn gave rise to phyllodineous species. If three genera are recognized it should be apparent that Racosperma sect. Univervia and sect. Pulchella have affinities with the rest of Racosperma not with Acacia or Senegalia. Both groups have derived characters and are among the most advanced members of Senegalia.

Senegalia and Racosperma are related to each other, but neither is particularly close to Acacia. The relatives of all three should be looked for among the Ingeae. The first two have some affinity with Paraserianthes (Albizia ser. Pachyspermae) and the last with Calliandra which itself appears to be paraphyletic. Investigation of the relationships of the genera of the Ingeae-Acaciae could be quite fruitful.

At present only a small proportion of species described as Acacia have names under Senegalia and Racosperma. The transfer of remaining names will be a major undertaking needing time and care. The ideal situation would be for Australian botanists to make the required new combinations for all Australian species in one place, avoiding taxonomy of the Rauschert kind. This is not likely to occur, but I am sure transfers of some names will be made. Individual workers will have to decide whether they refer newly described taxa to Acacia or the segregate genera. Change takes time but I do not believe that it will be 70 years before Racosperma and Senegalia are generally accepted as was the case with the segregate genera of Loranthus described by van Tieghem in the 1890's.

ASPECTS OF THE SYSTEMATICS OF THE EUCALYPTS

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The word has spread, both inside and outside the botanical community, that I and my colleagues are about to divide the long established genus Eucalyptus. There have been very definite attempts to pre-judge and to prejudice the outcome and acceptance of our work. I believe that judgements should be passed only when the work is complete and published, and is therefore available for evaluation.

Some critics have argued that existing concepts of Eucalyptus as a genus should be inviolate, claiming that they have stood the test of time. On closer consideration, as is often the case, one finds that very few workers have seriously reviewed this generic status, particularly in relation to the recognition of genera in the Myrtaceae as a whole. Most authors concerned with eucalypts have merely used existing taxonomic concepts and their work has not been such as to reveal any inappropriateness in delimitation or in levels of recognition.

The study on which I am engaged, with my colleagues Ken Hill and Don Blaxell, should be seen in the context of our approach to biological taxonomy generally and in relation to wider studies in the family.

Biological taxonomy tries to serve a number of masters and has several incompatible aims. Therefore it cannot be a fully scientific discipline. It has roots in folk taxonomy and in essentialism and is influenced by the demand to produce "practical" revisions and keys. Indeed emphasis on Flora production tends to promote its less scientific aspects. On the other hand, in its scientific phase, it seeks

1. to elucidate phylogeny and to produce classificatory systems that reflect phylogeny;
2. to study processes of evolutionary change and the adaptive syndromes that make evolutionary lineages discernible through morphology.

The eucalypt project is a comprehensive review (concise revision) of what we intend to treat as Tribes Eucalypteae and Arillastreae, which correspond respectively to the Eucalyptus Alliance and the Eucalyptopsis Alliance of Briggs & Johnson (1979), but with Arillastrum removed from the former of these to the latter, as indicated in Johnson & Briggs (1985, p.734). We shall deal with all levels from subspecies through species, superspecies, subseries, series, section, genus, and subtribe to tribe. Consideration of the generic level is a relatively small part in all of this.

The study follows phylogenetic studies of Myrtales and of Myrtaceae (Johnson & Briggs 1985). Those broader studies produced a phylogenetic hypothesis for the major groups in Myrtaceae that was radically different from traditional groupings within the family. It did not support the subfamilies Myrtoideae and Leptospermoideae. In our phylogram the eucalypt assemblage was seen as a well-marked lineage arising near the base of the family, whereas the former subfamily Chamelaucioideae, for example, appeared as an upper branch on the same stalk as the Leptospermum group.

In that analysis - as in our present work - the eucalypt group consisted of the traditional Eucalyptus together with Angophora, Arillastrum, Eucalyptopsis, Allosyncarpia and an undescribed north Queensland taxon allied to the last three of these.

The analysis was by the CLAX program which I have been developing with Chris Johnson. This program, now running on computer but which Barbara Briggs and I originally worked most laboriously by hand, does not allow unrestrained character reversal and so avoids many of the implausible character sequences that result from some programs. Considered character reversals can of course be taken into account.

The size of the eucalypt group, with probably more than 800 species, has prevented a full cladistic analysis at lower taxonomic levels. Our aim is phylogenetic, but at the lower levels cladistic trees would not necessarily be robust since distinguishing characters are sometimes few and it is evident that homoplasy is rife, as in so many plant groups.

At the higher taxonomic levels, around the level of the genera we now propose to recognise, cladistic study is more instructive and has been based on 70 characters over 15 groups. In such analysis a wide character spread is essential. For instance, to base too large a proportion of characters on seedling or juvenile stages could be almost as misleading as to fail to use any of these important features.

Some of the general results of the analysis, taken with the earlier work and the studies by Lindsay Pryor and myself that led to our recognition of subgenera (not then formally described) are as follows:

- the tribe Eucalypteae is probably not polyphyletic
- some groupings are robust, others less so, but we recognise three subtribes
- several alternative phylogenetic trees are little different in length
- there are robust groupings of recognisable and satisfying assemblages within each of the subtribes.

Thus there are three levels at which consistent classifications are possible: (1) the tribe, (2) the subtribes and (3) the level now proposed for generic recognition.

Recognising three genera (at the level of our proposed subtribes) has no real advantages. It does not preserve existing nomenclature (e.g. the name Angophora is retained but with a different circumscription, covering the traditional Angophora together with the bloodwoods and ghost gums). The three groups are not as recognisable as their constituents that are our proposed genera. Moreover there is still some doubt as to the coherence of one of the three groups.

We are then left with two possibilities. Either we recognise the segregate genera or we must logically accept a single genus to encompass the whole tribe. The latter might seem convenient but would involve "sinking" Angophora. Worse, it gives a "genus" which in age (since the lineage comes from near the base of the family) and diversity of

morphology and ecology is equivalent to suprageneric groupings elsewhere in the family. Some of these suprageneric groupings consist of large numbers of genera that have customarily been accepted.

Like any major taxonomic reassessment, division of Eucalyptus will produce some upheaval and at least some temporary communication problems. However, these have often been overstated.

Within botanical systematics it should be recognised that large taxa that are commercially and ecologically important should be treated by the same scientific standards as less prominent groups (and it is interesting how little objection is raised to the division of less prominent genera like Cyperus, Bassia or Baeckea). Outside systematics the desire of native plant enthusiasts, foresters and others to follow scientifically approved nomenclature or to be up-with-the-latest in usage will help to shorten the changeover period.

A substantial spin-off benefit of the new generic usage will be the greater information content of the segregate generic names. They refer to groups that have characteristic geographic and ecological distribution patterns. Description of the flora of different parts of Australia will be more informative when these names are in use. On the other hand "eucalypt" can still be used generally for any or all of the tribe in less precise contexts.

This study is not yet finished, so where do we go from here? In the field and in the herbarium my colleagues and I are reviewing the taxa. We are in discussion with most botanists who are looking at the identity and status of various groups, and are actively but without prejudice reviewing the work of some others who are not involved in such discussion. This work is showing up many new taxa. Some are newly discovered; even more are already in collections but were not previously distinguished as groups warranting recognition. We hope to go from this to more detailed cladistic studies - but that is for the future.

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, though the numerous new combinations required have never been made. For such a move to be generally acceptable, the paraphy-
lysis of

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